BEHAVIORAL AND BRAIN SCIENCES (2009) **32**, 1–67
Printed in the United States of America
doi:10.1017/S0140525X09000016

Sex, attachment, and the development of reproductive strategies

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Abstract: This target article presents an integrated evolutionary model of the development of attachment and human reproductive strategies. It is argued that sex differences in attachment emerge in middle childhood, have adaptive significance in both children and adults, and are part of sex-specific life history strategies. Early psychosocial stress and insecure attachment act as cues of environmental risk, and tend to switch development towards reproductive strategies favoring current reproduction and higher mating effort. However, due to sex differences in life history trade-offs between mating and parenting, insecure males tend to adopt avoidant strategies, whereas insecure females tend to adopt anxious/ambivalent strategies, which maximize investment from kin and mates. Females are expected to shift to avoidant patterns when environmental risk is more severe. Avoidant and ambivalent attachment patterns also have different adaptive values for boys and girls, in the context of same-sex competition in the peer group: in particular, the competitive and aggressive traits related to avoidant attachment can be favored as a status-seeking strategy for males. Finally, adrenarche is proposed as the endocrine mechanism underlying the reorganization of attachment in middle childhood, and the implications for the relationship between attachment and sexual development are explored. Sex differences in the development of attachment can be fruitfully integrated within the broader framework of adaptive plasticity in life history strategies, thus contributing to a coherent evolutionary theory of human development.

Keywords: adrenarche, attachment, cooperative breeding, evolution, life history theory, mating, middle childhood, phenotypic plasticity, reproductive strategies, sexual selection, stress

1. Introduction

1.1. Aim and scope

In this article, I present an integrated evolutionary model of the development of attachment and reproductive strategies in humans. The model is built on the foundations of life history theory, parental investment theory, and sexual selection; it aims to provide a significant update to current life history models of attachment formulated by Belsky and colleagues (Belsky 1997a; 1999; Belsky et al. 1991) and Chisholm (1999). In particular, the model I describe is the first to explain the development of sex differences in attachment patterns, permitting tighter integration between attachment theory, human reproductive ecology, and behavioral endocrinology.

The gist of life history models of attachment (reviewed in sect. 5) is that infants and young children use their parent's caregiving behavior as an indicator of the safeness and predictability of their local environment. Attachment security is the result of this unconscious evaluation process; the degree of security experienced in the first 5–7 years is hypothesized to set development on alternative developmental pathways, and to adaptively shape the individual's future reproductive strategy. Secure attachment should lead to reproductive strategies based on late maturation, commitment in long-term relationships, and higher investment in parenting. Insecure attachment, on the other hand, should lead to strategies based on early reproduction, short-term mating orientation, and lower parental investment in a larger number of children.

My contribution extends the above-sketched theoretical framework by making a series of new points, which I briefly synthesize here.

1. *Sex differences in attachment have adaptive significance*. I argue that sex differences in attachment patterns arise as a result of asymmetries in parental investment and sexual selection, and that they are adaptive both in children and in adults. Previous theorists (e.g., Belsky 1999) have tried to make adaptive sense of the differences between avoidant and ambivalent attachment, but the link between attachment patterns in childhood and adult

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0140-525X/09 $40.00

reproductive strategies is still poorly understood. I will show that taking sex differences into account makes it possible to reconcile individual differences in insecure attachment patterns with the concept of sex-specific reproductive strategies.

2. *Sex differences in attachment arise in middle childhood*. I present evidence that sex differences in attachment patterns are found not only in adults but also in children, starting from about 6–7 years of age (see also Del Giudice 2008). The available data suggest a phase of sex-biased reorganization of the attachment system in middle childhood, with a majority of insecure females shifting to ambivalent attachment and most insecure males shifting to avoidant attachment.

3. *Sex-related endocrine mechanisms can influence the development of attachment patterns*. Finally, I propose a hypothesis about the hormonal basis of the middle childhood transition in the organization of attachment. I review evidence showing that middle childhood is marked by intense, sex-related endocrine activity, and that the interplay between sexual maturation and attachment might be deeper and more bidirectional than is currently acknowledged. This view of attachment is also consistent with recent evolutionary models of the stress response system, suggesting intriguing avenues for cross-disciplinary research.

1.2. Overview of the target article

Because the idea of middle childhood as a transitional phase implies a degree of discontinuity in the development of attachment, I begin by sketching the issue of continuity versus change in attachment theory (sect. 2), and by linking it to the general biological problem of trait continuity across different life stages (sect. 3). Then, I summarize current evidence regarding sex differences in attachment, from infancy to adulthood (sect. 4). After reviewing extant life history models of attachment (sect. 5), I describe how sexual asymmetries in reproduction and sexual selection can be included in the picture to account for sex differences in reproductive strategies. I then discuss the resulting implications for attachment theory (sect. 6). Finally, I outline an updated synthesis of the development of human attachment and reproductive strategies, and explore the possible hormonal basis of the changes observed in middle childhood (sect. 7).

2. Continuity and change in attachment

2.1. Attachment as an evolved motivational system

Attachment theory, pioneered by John Bowlby (1969/1982; 1973; 1980), is to date the most comprehensive account of the nature and development of child–caregiver relationships. In addition, it embeds a complex theory of personality development, and has many implications for the study of social adjustment, emotion regulation, couple relationships, and psychopathology (see Cassidy & Shaver 1999, for an overview). According to attachment theory, infants are innately motivated to form selective emotional bonds with their caregivers, and organize their own behavior in order to seek and maintain proximity to them. Attachment is thus conceptualized as an innate behavioral–motivational system, with the evolved function of protecting the child from danger while motivating the caregiver to provide for the child.

Whereas the attachment system is a universal characteristic of human beings, there is much individual variation in the organization of actual attachment relationships. The systematic study of such variation started with the work of Ainsworth et al. (1978) and led to the concept of attachment patterns. Following early experience, infants adjust their care-eliciting behavior in order to maximize the caregiver's availability; the resulting patterns – ranging from clingy, anxious care-seeking to apparently detached and distancing behaviors – are found cross-culturally (van IJzendoorn & Sagi 1999) and seem to represent the basic human ways of organizing parent–infant relationships (see Suomi 1999, for a description of similar patterns in other primates). Individual differences in attachment relationships have profound consequences for the child's social and emotional development; hundreds of studies have been carried out to identify the causes of such differences, their developmental outcomes, and their mechanisms of change.

2.2. Patterns of attachment

A central notion in attachment theory is that relationships with caregivers become internalized as *internal working models* (IWMs), which are described as sets of beliefs and expectations about the self, the world, and relationships, together with rules for the direction of behavior and the appraisal of experience. IWMs guide the child's interpersonal behavior, and are at the root of individual attachment patterns, or "styles" (see Ainsworth et al. 1978; Weinfield et al. 1999, for detailed descriptions). Children experiencing a consistently available, sensitive caregiver who is able to tune in to their states and feelings develop a *secure* attachment (labeled B); they use their caregiver as a "secure base" for exploration and, when distressed, turn to him or her for help and are easily comforted. In European and North American low-risk samples, the normative proportion of secure infants is about 65%, with remarkable consistency across different countries (see van IJzendoorn & Sagi 1999, for a review).

Children who experience a rejecting, cold, and uninvolved caregiver establish an *insecure–avoidant* attachment pattern (labeled A): They treat the caregiver as unavailable, tend to avoid physical contact, and when distressed, don't ask for help or comfort. They are adopting a "minimizing" or "deactivating" behavioral strategy, since signalling distress and need would lead to further rejection. On average, about 25% of infants in Western samples are classified as avoidantly attached, but proportions vary in different countries.

If the caregiver is inconsistently available, alternating acceptance and rejection and being scarcely tuned to the child's needs, the child is expected to develop an *insecure–ambivalent/resistant* attachment (labeled C). Ambivalent children are easily distressed and ask vigorously for help and comfort, but are not easily calmed and protest angrily in order to maintain closeness with the caregiver. Their attachment strategy can be described as "maximizing," "hyperactivating," and overdependent, since they exaggerate their signalling of need in order to control the caregiver's behavior. The proportion of ambivalent infants is about 10% on average, again with some cross-cultural variation.

Sometimes, the child faces caregivers who are frightening or threatening in their parental behavior. Frightening behaviors can range from sudden, trance-like dissociative states, resulting from traumatic experiences or unresolved losses on the parent's side, to downright physical or sexual abuse. Such caregiver's behaviors tend to disrupt the child's attachment strategy, leading to more or less severe forms of *disorganization*. Disorganized children (labeled D) may show elements of the previously described attachment strategies, but they experience abnormally high levels of motivational conflict, since the caregiver is simultaneously a source of comfort and fear. This results in conflicting approach/avoidance displays, dissociative states (e.g., "freezing"), and intrusion of sudden aggressive actions directed at the caregiver (Hesse & Main 2006; Lyons-Ruth & Jacobvitz 1999; Lyons-Ruth et al. 1999; Main & Hesse 1990). The proportion of disorganized children is highly variable across samples, and can range from 10%–15% in low-risk families to 70% or more in extremely high-risk settings.

Attachment patterns can be described either as categorical types, as I have done here, or as dimensional constructs. While many researchers rely on assessment procedures yielding categorical three-way (ABC) or four-way (ABCD) profiles, some have proposed that a better understanding of attachment dynamics is gained by assessing individual styles as combinations of underlying dimensions, such as high–low anxiety and high–low avoidance. Many researchers adopt some combination of the two methods; in particular, attachment security and disorganization are often described (and measured) as continuums rather than categories. I will not pursue the issue further here; for an overview of the ongoing debate, see Fraley and Spieker (2003) and related commentaries (Cassidy 2003; Cummings 2003; Sroufe 2003; Waters & Beauchaine 2003).

2.3. Longitudinal studies

Internal working models (and their corresponding behavioral patterns) are thought to be somewhat persistent and self-sustaining, but, at the same time, open to revision in the face of changing relational experiences (Bretherton & Munholland 1999). The question, then, is to what extent do IWMs persist (even across generations) rather than change or adjust to new conditions and life events. Of course, a detailed treatment of the issue is beyond the scope of this article; excellent reviews can be found in Grossmann et al. (1999), in the journal *Child Development* (2000, vol. 71), and in Grossmann et al. (2005). The growing consensus among attachment theorists is that stability in attachment is strongly tied to stability in caregiving conditions (e.g., Allen & Land 1999; Waters et al. 2000). Social stressors and negative life events (such as illness or death of relatives, changes in living arrangement, parental divorce, abuse, etc.) are associated with instability of attachment patterns from infancy to early adulthood; in particular, they lower stability by increasing the likelihood of shifting from secure to insecure attachment styles during development (see Hamilton 2000; Lewis et al. 2000; Waters et al. 2000; Weinfield et al. 2000). On the other hand, low-risk samples in relatively stable conditions can yield high degrees of consistency between infant and adult attachment security (even in the 70% range; e.g., Waters et al. 2000). A classic three-generation study by Benoit and Parker (1994) provided an extreme example of stability, with 75% concordance between infants and their grandmothers on three-way attachment classifications. A general pattern seen in longitudinal studies is that attachment security is more stable and predictable than specific insecure strategies (e.g., avoidant or ambivalent) are. It is possible, then, that attachment security is at the "core" of lifelong IWMs, with specific A/C patterns providing a fine-tuned (and somewhat contingent) response to current caregiving style and ecological circumstances. This idea is pursued further in sections 6 and 7.

Recently, Fraley (2002) performed the first meta-analysis of stability in attachment security from ages 1 to 21, and, in the same pioneering study, attempted to test two mathematical models of the underlying process of change. His results confirmed the association between psychosocial risk and stability: The overall correlations between security at age 1 year and subsequent ages were estimated at .48 for low-risk samples and .27 for high-risk samples (stability of specific attachment patterns was not assessed). Thus, this meta-analysis provided evidence of moderate stability, especially in low-risk samples; as discussed earlier, the lower stability associated with high-risk samples is not random, but reflects frequent shifts towards greater insecurity. Comparing the predictions derived from his mathematical models to the meta-analytic data, Fraley found support for a prototype model of stability, in which early security continues to influence security at later ages without being overridden; the model was tested against a so-called revisionist model, which instead assumed no persisting effect of early security. The model, of course, does not tell which factors are responsible for such prototype-like dynamics; likely candidates are early experience, strong continuity in rearing environment, and heritable genetic factors.

Evidence from twin studies shows that attachment in infants and young children is mainly influenced by shared and non-shared environmental effects (note that nonshared environmental effects may also include genotype-environment interactions, and thus do not exclude broad-sense genetic influences on attachment stability), with no or little additive genetic contribution (Bakermans-Kranenburg et al. 2004; Bokhorst et al. 2003; O'Connor & Croft 2001; O'Connor et al. 2000; but see Finkel et al. 1998). In contrast, two studies with adult twins (one using the Adult Attachment Interview [AAI] and one using the Relationships Questionnaire [RQ]; see sect. 2.4) both found moderate heritability in attachment security and style (Brussoni et al. 2000; Torgersen et al. 2007). Thus, it seems that genetic factors may contribute to discontinuity rather than continuity in attachment, with additive genetic factors becoming more influent in adulthood.

2.4. The assessment of attachment from infancy to adulthood

An additional source of complexity in the study of attachment is that measures developed for a given age group typically cannot be employed at other ages. This has led to a variety of assessment methods, some based on actual behavior, some on behavior representations (e.g., stories, doll play), and others still on interviews or questionnaires. All tend to retain the core construct of attachment security, but insecure styles may be categorized in different ways that are not always directly comparable. For in-depth reviews of the topic, I refer the reader to Solomon and George (1999), Crowell et al. (1999), and Kerns et al. (2005). As children grow up, the focus of measurement tends to shift from observed behavior towards behavior representations; some tasks are predominantly verbal, whereas others include "behavioral" aspects (e.g., doll-play procedures). Nevertheless, most childhood measures can be easily mapped onto the classic ABCD classification. From adolescence on, however, two distinct approaches to the assessment of attachment exist, and they differ substantially in scope and results.

2.4.1. Measures of adult attachment. The first approach is based on interviews like the Adult Attachment Interview (AAI; see Main & Goldwyn 1998). These interviews do not assess present attachment behavior, rather focusing on the "mental state" with respect to past attachment experiences, inferred by discourse analysis. The AAI categories ("free," "dismissing," "entangled," and "unresolved") refer to how the person relates to his or her own past experiences with parents, not to the way he or she behaves with present attachment figures (see Hesse 1999). Adult AAI categories are reliably associated with the attachment classification of sons and daughters (e.g., entangled parents tend to have ambivalently attached children; see Belsky 2005, for a review).

The second approach, often referred to as "social psychological," is based on self-report questionnaires and is mostly employed in research on romantic (couple) attachment. Compared with interviews, most questionnaires are conceptually closer to childhood measures, because (1) they focus on present behavior and feelings towards romantic partners, and (2) their classification of insecure attachment is modeled on the avoidant and ambivalent patterns of infancy. Analysis of many self-report attachment questionnaires reveals two robust dimensions underlying romantic attachment patterns, labeled *avoidance* and *anxiety* (Brennan et al. 1998). Secure adults (low avoidance, low anxiety) feel it easy to get emotionally close to others, feel comfortable depending on someone else, and do not worry much about rejection. Dismissing-avoidant adults (high avoidance, low anxiety) are distancing with their partners, show a low need for intimacy and closeness, and describe themselves as self-sufficient. Preoccupied adults (low avoidance, high anxiety) report intense desire for closeness, feel uncomfortable when not being involved in close relationships, and worry about partner's rejection. Finally, fearful-avoidant adults (high avoidance, high anxiety) show a mix of desire for closeness and fear of rejection, and they report feeling uncomfortable in depending on others.[1]

Interviews and questionnaires show only low to moderate correlations with one another, usually below $r = .30$ (Crowell et al. 1999; Roisman et al. 2007; Shaver et al. 2000); in addition, they seem to predict somewhat different outcomes. Roughly stated, interviews are most powerful at predicting parenting outcomes such as children's security (and indeed have been originally devised to this end), whereas questionnaires are more predictive of mating outcomes, such as couple stability, satisfaction, and sexual behavior (e.g., Bernier & Dozier 2002; see further in the target article). The two aspects, of course, are not completely independent, and they show some overlap (especially on the security–insecurity dimension). There has been considerable debate on the relative merits of one approach over the other (e.g., Belsky 2002; George & West 1999; Shaver & Mikulincer 2002); in particular, questionnaire studies have been criticized because there was no evidence linking the attachment styles they measure to specific developmental antecedents (Belsky 2002).

3. The general problem: Trait continuity across life stages

Although seldom realized, the issue of attachment stability can be seen as an instance of a more general biological problem: that of continuity of phenotypic traits across different life stages. Attachment patterns are described as (relatively) coherent behavioral strategies, affecting not just the relationship with caregivers but also a wide range of developmental outcomes and processes, such as aggression, social competence, and emotion regulation (see Thompson 1999, for a review). As such, they are trait-like parts of the behavioral phenotype, and are clearly capable of affecting an individual's biological fitness. As stressed by Belsky (1999), the ultimate fitness effects of a trait are to be understood in terms of reproduction, both of the individual itself and of its genetic relatives (the inclusive fitness concept; Hamilton 1964). However, early attachment theorists (e.g., Bowlby 1969/1982; Cassidy & Berlin 1994; Hinde 1982; Main 1981; 1990) have selectively emphasized the survival value of attachment (i.e., eliciting protection and parental investment from caregivers), even if survival is only an intermediate (and sometimes unnecessary) step towards evolutionary fitness. Life-history theory approaches, on the other hand, focus exactly on the reproductive consequences of attachment, and I review them in section 5. Before getting to reproduction, however, it will be useful to discuss the problem of trait stability in some detail.

3.1. Discontinuity across life stages

Psychologists often assume that development is an essentially cumulative process, in which each stage builds on the preceding ones, and previous characteristics (especially in the behavioral domain) have a natural tendency to persist unless actively modified. Even if this makes intuitive sense, it is important to realize that, from the point of view of natural selection, such continuity is neither necessary nor always useful (see also Bjorklund 1997; Geary & Bjorklund 2000, for a general introduction to this topic). In many species, development involves dramatic alterations in shape and behavior, as, for example, the metamorphosis process that turns tadpoles into frogs; furthermore, many developmental transitions involve the loss or disposal of previous phenotypic characters (such as the tadpole's tail). Although humans do not undergo such radical metamorphoses as frogs, a careful look at human development does reveal many subtler examples of the same principle, both in morphology (e.g., detachment of the placenta, replacement of milk teeth, loss of brown fat in adults) and in behavior (e.g., loss of neonatal reflexes, abandonment of quadruped locomotion).

The key to understanding such apparent exceptions to the cumulative nature of development is to look at developmental traits (morphological as well as behavioral) from a fitness perspective. In order to be selected for, traits need to solve two problems: being adaptive at the present time and being adaptive in the future of the organism. Sometimes, the solution of the puzzle is to build "disposable" traits, or *ontogenetic adaptations* (Bjorklund 1997), which are only adaptive during certain developmental stages and are replaced or modified when necessary. In this way, development becomes "modularized," and selection can act independently on different life stages (see Wilkins 2002; West-Eberhard 2003, for the concept of modularity in development). In altricial mammals like humans (which are born immature and undergo an extended period of parental care), some infantile traits could be selected for because they are adaptive in the context of parental care; on the other hand, the same traits might become useless, or even maladaptive, when the individual becomes independent (see also Lynch [1987] for a genetic approach to the same problem). Selection is expected to act on traits such as these by rendering them transient (i.e., disposable), so that aspects of the phenotype that are no longer necessary are lost, or replaced, during maturation.

3.2. Continuity across life stages

At the same time, continuity is a major feature of development. There are many reasons for this, including continuity of environment and ecology during growth and the costs involved in switching and reshaping phenotypes (Bateson 2005; Boyce & Ellis 2005; Ellis et al. 2006). Yet another powerful source of continuity in development, even across modularized life stages, is that it is often adaptive for an organism to rely on early outcomes to make strategic decisions about the next developmental phases it will face. A classic illustrative example comes from male dung beetles, whose development involves a neat binary switch between two alternative phenotypes (or "morphs"). The nutritional condition of a beetle's larva, determined by maternal food supply, is strongly predictive of the beetle's adult body size; body size, in turn, determines whether the individual is to develop horns (and fighting behavior) or not. The whole process is orchestrated by hormonal mechanisms. As a result, there are two kinds of males in the population: those who can afford the metabolic expense of growing horns and fighting, and those who are better off if they "decide" in time to adopt a less costly developmental strategy, together with different reproductive behaviors (Emlen 1997; West-Eberhard 2003).

In this sense, previous development provides the organism with useful information, which can be used to direct the next phases in an adaptive way. Sometimes it is possible to identify developmental "switch points" between alternative pathways (see also Hagen & Hammerstein 2005), while at other times the process looks more gradual. What is important to keep in mind is that stability in phenotypic traits is not to be taken for granted, and must always be weighted against developmental tradeoffs between present and future contributions to reproductive success.

3.3. Parent–offspring conflict and the adaptive value of childhood traits

When the environment in which selection takes place includes genetic relatives of the developing organism, additional issues arise. Most relevant for the present discussion is the concept of parent–offspring conflict (Mock & Parker 1997; Parker et al. 2002; Trivers 1974), which is the conflict of interest between parents and offspring about the amount of investment (e.g., energy, time, food) to be provided in parental care. Parent–offspring conflict follows from the fact that, while an offspring is perfectly related to itself, its relatedness coefficient with siblings (i.e., the probability of sharing an allele by common descent) is only 0.5. Although a parent optimizes its inclusive fitness by investing the same amount of resources in each offspring (all else being equal), a single offspring maximizes its own fitness by requiring a higher amount for itself, as the benefits enjoyed by siblings must be discounted by their relatedness coefficient. The bottom line is that costs and benefits of a given amount of parental investment will not affect the fitness of parents and offspring in the same way. This concept, originally formulated to explain patterns of parental investment, can actually be extended to a much more general principle: Parents and offspring will value differently every developmental outcome (including those unrelated to parenting), provided that benefits gained by one side translate into fitness costs to the other, even indirectly. Trivers (1974), for example, suggested that parents and offspring can disagree about offspring's degree of altruism (towards both kin and nonrelatives), mate choice, and reproductive effort.

Following this line of reasoning, Trivers (1985) suggested a non-obvious implication of the theory. He suggested that offspring should not allow themselves to be permanently influenced by parental behavior, as the genetic interest of parents ultimately differs from their own. Referring to human development, he speculated that "compliance" with parental influence should last until the end of dependency, and then be erased during puberty through a sort of personality reorganization. In this view, childhood personality traits influenced by parents (and attachment patterns certainly fall into this category) are exactly the kind of disposable behavioral phenotypes described above; they are adaptive in the limited context of parental care, but need to be modified or replaced in the transition to adulthood. The idea is quite powerful, and it has been reprised by critics of "family socialization" theories of personality development such as Harris (1995; 2005) and Pinker (1997) to argue that parents should not be expected to permanently shape their children's personality. However, there are a number of biological reasons to doubt a "black-and white" approach, and to predict a more balanced mix of continuity and discontinuity. First, it is true that genetic interests of parents and offspring differ, but there is still quite a lot of overlap, so that a certain degree of parental "shaping" can be expected. Second, the conflict hypothesis only applies to cases in which parental influence involves costs (or benefits) on the parents' side; cost-free parental influence is not expected to lead to this kind of conflict. Third, parental behavior can sometimes provide offspring with indirect information about the state of the local environment; in other words, offspring may use parental behavior as a proxy for external ecological conditions, even independently from the parent's willingness to provide such information (see Bateson 2005; Chisholm 1993; Draper & Harpending 1982; Ellis et al. 2006).

Life history models of attachment, which predict strong continuity between attachment patterns in childhood and adult behavior, are essentially based on the latter assumption: Because parental behavior carries useful information about the local ecology, children can be responsive to their rearing environment to the point of basing their adult reproductive strategy on early attachment experience. However, it doesn't follow that a child becoming an adult should employ the same behavioral strategy which proved useful with parents in his or her early childhood. One reason is that, in humans, the attachment system is not just a care-eliciting mechanism for the young – it has also been recruited by evolution to serve as a powerful pair-bonding device in the mating couple.

3.4. *The double life of human attachment*

The "double life" of the attachment system, as a care-eliciting and pair-bonding device, is a central theme of the present discussion. Attachment theorists have realized from the start that infant–caregiver bonding and couple relationships share many key features, so that adult love can be properly characterized as involving an attachment dimension (in fact, intimate friendship may also be characterized as attachment relationships, so that human attachment can be said to have "multiple lives"; see, e.g., Sibley & Overall 2008). Research has shown that the dynamics of bond formation, separation, and loss in adults are strikingly similar to those observed in infants (for reviews, see Feeney 1999; Hazan & Zeifman 1999). Neurobiological studies also suggest that the neurochemical/neuroanatomical substrates involved are largely overlapping (see Carter 1998; Insel 2000; Insel & Young 2001; Leckman et al. 2005; Panksepp 1998; Pedersen et al. 2005).

Similarities notwithstanding, the two processes are not identical (see Simpson 1994), and they are subject to different selective pressures. In particular, as I discuss in depth in section 6, attachment-related traits are expected to show sex differences in adults but not in young children, so that (for example) a detached, uncommitted, low-investment relationship style would usually be more advantageous to men than to women (e.g., Kirkpatrick 1998). Behavioral correlates of attachment patterns (e.g., dependency, aggression) would also have quite different fitness consequences in infancy and in adulthood if they happened to be involved in mate choice or sexual competition. For example, fearfulness and overdependency (related to ambivalent attachment) are likely to be equally adaptive for males and females in infancy, when they only affect the regulation of parental care. In adults, however, the balance could shift dramatically: If, for example, fearful/overdependent males (but not females) were less desirable as partners, and/or less able to compete with other males for status, the fitness consequences of attachment would no longer be neutral with respect to sex. It is wise, then, to ask whether sex differences in attachment have been found, what they are, and when they appear in the course of development.

4. Sex differences in attachment

4.1. *Infancy and early childhood*

The first decades of attachment research were characterized by the almost complete absence of reported sex differences in attachment security and style. This was due to a prevailing focus on infants and preschoolers, who usually do not show sex differences in attachment (e.g., van IJzendoorn 2000). Studies with children as old as 6 years usually find a comparable proportion of avoidant and ambivalent children in both sexes (e.g., Moss et al. 1998). The only exceptions were a few studies with high-risk samples, in which boys were found to be more frequently and/or more severely disorganized than girls (Carlson et al. 1989; Lyons-Ruth et al. 1999). Moreover, Turner (1991) found some behavioral differences in peer relationships between insecurely attached 4-year-old boys and girls: Insecure males were more aggressive and attention-seeking, whereas insecure females were more compliant, dependent, and affiliative.

Another report of small sex-related effects came from the meta-analysis by van IJzendoorn (2000), who found that siblings of the same sex were more likely to be both secure or both insecure, compared with mixed-sex pairs. More recently, David and Lyons-Ruth (2005) reconsidered sex differences in disorganization in the light of sexually dimorphic responses to stress and threat ("tend-and-befriend" versus "fight-or-flight"; Taylor et al. 2000; more on this in sect. 7.2.2). In a low-income infant sample, the researchers found different behavioral patterns in males and females consistent with the "tend-and-befriend" hypothesis: specifically, females responded with more approach displays than males when faced with frightening or threatening maternal behaviors.

4.2. *Middle and late childhood*

The picture changes dramatically when one considers middle childhood. To my knowledge, nearly all of the studies in which sex was examined have revealed significant biases in the avoidance-ambivalence dimension. This result holds across nations (to date: USA, Canada, Italy, Israel, and perhaps Hungary) and across assessment methods (questionnaires vs. doll-play procedures).

Granot and Mayseless (2001) performed a study on 113 Israeli children aged 9 to 11 years, with a doll-play task (an adapted version of the Doll Story Completion Task by Bretherton et al. 1990). The study focused on the relationship between attachment and school adjustment. Results showed an unanticipated sex difference: boys and girls differed significantly in their prevailing insecure patterns, with girls more often ambivalent than avoidant (18% C to 7% A on the total number of girls), and all of the insecure-organized boys classified as avoidant (27% A to 0% C on the total number of boys).

I found the same effect in an Italian sample of 122 7-year-old children (Del Giudice 2008), using a different doll-play task, the Manchester Child Attachment Story Task (MCAST; Green et al. 2000). Almost all insecure boys were classified as avoidant (27% A to 2% C), while insecure girls were mostly ambivalent (25% C to 4% A). The similarity of attachment distributions between Italy and Israel is even more striking since infant studies in Israel, but not in Italy, usually find a high proportion of ambivalent (17–37%) and a very low proportion of avoidant (0–7%) patterns (Harel & Scher 2003; Sagi et al. 1985; 1994; van IJzendoorn & Sagi 1999). Sex effects were also apparent in the distribution of secure subtypes; boys were more often classified as secure/avoidant than secure/ambivalent (46% B/A vs. 21% B/C), and girls showed the opposite pattern (32% B/C vs. 16% B/A). However, this effect was much weaker than that observed in insecure children. In the same study, I found that boys tended to get higher disorganization scores than girls, thus confirming the findings obtained with younger children by Carlson et al. (1989) and Lyons-Ruth et al. (1999).

Toth et al. (2006) used the MCAST in a Hungarian sample of 84 six-year-olds. Although the sample was somewhat younger than the others cited here, their results seem to show a smaller effect in the same direction (I. Toth, personal communication, October 19, 2007). The proportion of ambivalent and avoidant girls was the same (6%), whereas in males, the proportion of avoidant children (14%) was higher than that of ambivalent ones (2%). Unfortunately, the very low frequency of non-D insecure patterns in this sample (14% overall) makes statistical comparisons uninformative (in contrast, disorganization was significantly more frequent in boys than in girls: 47% vs. 20%).

Marked sex differences in middle childhood were also found in three studies using a self-report questionnaire on attachment behaviors, the Coping Strategies Questionnaire (CSQ). The first study was performed in the United States by Finnegan et al. (1996), with a sample of 229 children aged 8–13 years. In this study, boys reported significantly higher scores of avoidant coping, whereas girls reported more preoccupied coping. The authors noted this association with sex and attributed it to gender stereotyping.

Similar results were obtained in a Canadian study (Karavasilis et al. 2003), which investigated the relation between parenting and attachment to mother in a sample of 202 children aged 9–11 years. Boys reported more avoidant coping, while girls reported more preoccupied coping at the CSQ; both associations were statistically significant and of remarkable size.

In another US study, Corby (2006) administered an expanded version of the CSQ to 199 children aged 8–14 years (mean age: 11). Again, she found significantly higher avoidance scores in boys and higher preoccupation scores in girls.

The only contrasting result so far comes from a recent study in the United States by Kerns et al. (2007), in which the doll-play procedure used by Granot and Mayseless (2001) was administered to a sample of 52 children aged 9–11 years. In this study, (K.A. Kerns, personal communication, December 12, 2007), females were more likely to be classified as avoidant than ambivalent (35% A vs. 4% C); the same was true for males, to a lesser degree (19% A vs. 4% C). Boys were more often classified as disorganized (42% of boys vs. 4% of girls). This is the only study which departed from the overall pattern, at least for females; note, however, that sample size was substantially smaller compared to the other studies.

There are three reasons for the relatively small number of relevant studies in this age group. First, the lack of age-appropriate measures and tasks has led attachment researchers to neglect middle childhood until recently, so the sheer number of studies in this age range is much smaller than in infants or adults (Kerns et al. 2000; 2005). Second, attachment studies in middle childhood often focus solely on the security–insecurity dimension, without assessing avoidant/ambivalent insecure styles. Third, many researchers still omit reporting and analyzing their data by sex, probably based on the tacit assumption that sex differences in children's attachment patterns do not exist. Hopefully, the accumulating evidence for strong sex effects in this age group will prompt more researchers to include this variable in their studies.

4.3. Adolescence and adulthood

When examining sex differences in adult attachment, the issue of measurement methods (interviews vs. questionnaires) becomes crucial. The first surveys of adult attachment styles were based on the AAI, and consistently failed to reveal any sex difference (e.g., van IJzendoorn & Bakermans-Kranenburg 1996). The same seemed to happen, at first, with questionnaire-based measures: indeed, most early studies failed to find significant sex differences in styles of romantic attachment (e.g., Collins & Read 1990; Feeney & Noller 1990; Hazan & Shaver 1987). However, early self-report attachment measures had a categorical response format and very low reliability (Baldwin & Fehr 1995). Newer studies, employing continuous ratings, soon began to find sex effects on attachment self-reports: notably, men (on average) have higher avoidance scores and lower anxiety scores than women, or (depending on the instrument) rate themselves as more dismissing (e.g., Bartholomew & Horowitz 1991; Brassard et al. 2007; Brennan et al. 1998; Kirkpatrick 1998; Picardi et al. 2002; Scharfe & Bartholomew 1994). Not all questionnaire studies found sex differences, however (e.g., Gentzler & Kerns 2004; Jang et al. 2002).

Questionnaire studies with adults often find smaller sex differences than those reported in middle childhood, especially compared to those found with doll-play procedures. Part of this effect may depend on the lower accuracy of self-reports compared with experimenter-coded measures (distinct from psychometric reliability, which is usually high). There is, however, a more interesting explanation: When age is taken into account, it becomes apparent that sex differences are stronger in young adulthood and decline markedly approaching middle age. In a large Italian validation sample for the ECR (Experiences in Close Relationships; Brennan et al. 1998), for example, standardized sex differences in the anxiety dimension were $d = .57$ at 18–20 years, $d = .48$ at 21–35 years, and $d = -.02$ at 36–65 years (Picardi et al. 2002). The same age-related decline of sex differences was apparent in the cross-cultural study by Schmitt et al. (2003a; see following). Thus, depending on participants' age, the size of sex differences can vary considerably. I discuss the relevance of this finding in section 7.

Schmitt et al. (2003a) performed a cross-cultural study of adult attachment in 62 cultural regions employing the Relationships Questionnaire (RQ; Bartholomew & Horowitz 1991). While male and female dismissiveness scores were highly correlated across samples ($r = .87$), males described themselves as more dismissing than women in most countries, with smaller differences in Oceania and East Asia, and no significant difference in Africa. The overall effect size was $d = .18$. There was substantial cultural variation in the degree of sex differences (d ranging from $-.26$ to .43), and it was mostly driven by female dismissiveness scores. Smaller sex differences were related to higher dismissiveness (especially in females), and both were predicted by high levels of mortality, high fertility, and high AIDS rates, but not by indexes of gender inequality and cultural stereotypes. Overall, cultural stereotypes do not seem to explain much variation in sex differences, which appear to be more closely related to levels of environmental stress: where mortality and fertility are high, women (and, to a lower extent, men) are more dismissing, and sex differences tend to become smaller. Mean age in the 62 samples ranged from 19 to 38 years (median, 22 years; reported in Schmitt et al. 2004). I correlated the mean age of each sample with the corresponding effect size d; Pearson's correlation was negative and significant ($r = -.30$, $p = .016$, $N = 62$), showing that sex differences in dismissiveness get smaller with increasing age. (Of course, longitudinal data would be necessary to rule out cohort effects.)

5. Attachment and life history theory

5.1. Life history strategies

Life history theory (see Hill 1993; Kaplan & Gangestad 2005; McNamara & Houston 1996; Roff 2002) is a branch of theoretical evolutionary biology, dealing with the trade-offs in the allocation of time and resources over an organism's life span. The starting point of life history theory is that time and resources are inherently limited, so organisms have to make decisions about how to invest them to optimize their fitness. The way resources are allocated constitutes the organism's life history strategy. Different ecological constraints will result in different optimal strategies, both at the between-species and at the within-species level.

The basic trade-off in life history theory is that of *somatic effort* versus *reproductive effort*. The former is defined as resources devoted to growth during development and maintenance during adulthood; it also includes the accumulation of resources that augment the reproductive potential. The latter is typical of mature stages and is distributed between *mating effort* (resources invested to attract mates, increasing opportunities for reproduction) and *parenting effort* (resources invested in raising already-conceived offspring). The balance between mating and parenting is another key trade-off in life history strategies.

Another way to conceptualize life histories is by considering two reproduction-related trade-offs: between *current* versus *future* reproduction and between *quality* versus *quantity* of offspring (for an introduction, see Chisholm 1993; Hill 1993; Pennington & Harpending 1988). The optimal solution of these trade-offs is related to the ecological pattern of extrinsic mortality, that is, mortality that cannot be prevented or diminished by altering the organism's behavior. Predation, pathogens, and warfare are usually considered extrinsic sources of mortality; but, more generally, all factors that negatively affect reproductive success independent on the organism's decisions can be considered sources of *extrinsic risk* (Quinlan 2007). When adult mortality is high, it is adaptive to favor current reproduction by starting mating early, even at a cost for one's future reproductive potential (costs may arise, for example, because waiting longer gives higher benefits to offspring, or because reproducing earlier increases parent's mortality). When juvenile mortality is high, it pays for parents to avoid the risk of lineage extinction by producing more offspring and investing fewer resources in each (Promislow & Harvey 1990; 1991). In addition, high extrinsic risk means that investing in parental care has quickly diminishing returns: Since (by definition) parental effort cannot decrease extrinsic risk, offspring's fitness will not respond to parental care beyond a certain amount (the "saturation point"; see Fig. 1). Thus, elevated environmental risk favors quantity versus quality of offspring and current versus future reproduction, and selects for life histories that invest in mating at the expense of parenting (Chisholm 1993; Pennington & Harpending 1988; Quinlan 2007).

5.1.1. The human life history. When compared with other species, humans show many traits characteristic of an extremely "slow" life history strategy. We reproduce late, and pass through a prolonged stage of reproductive immaturity which has no equivalent in other primates (Ellison 2001; Flinn & Ward 2005). Moreover, we invest considerable time and effort in parental care, which involves a lot of teaching and social training in addition to mere energetic investment (Bjorklund & Rosenberg 2005; Geary & Flinn 2001; Hewlett et al. 2000). As an exception to this pattern, humans show high fertility compared with their close primate relatives, with inter-birth intervals of about 2.5–3.5 years. The peculiar pattern of human life history traits can been explained by the coevolution of a bigger brain, extended skill learning and slow growth rate in childhood, longevity, and skill-intensive foraging practices such as hunting and complex food processing. This suite of characters leads to a unique combination of high fertility and slow development, obtained through massive intergenerational transfer of resources (see Gurven & Walker 2006; Kaplan et al. 2000; Kaplan & Robson 2002). In addition to the need for extended learning of foraging

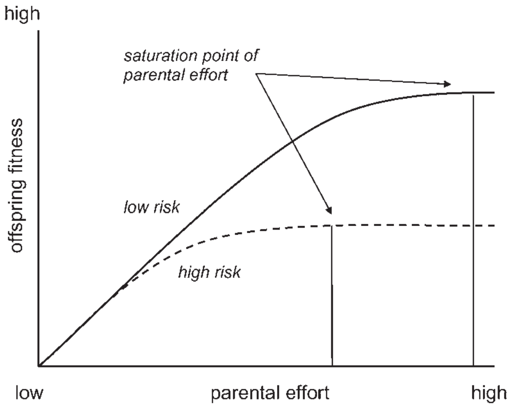

Figure 1. Effect of extrinsic risk on offspring fitness as a function of parental effort (adapted from Quinlan 2007). Increased extrinsic risk (dashed line) lowers the saturation point of parental effort (i.e., the point at which additional effort does not increase offspring fitness).

abilities, the social complexity of human coalitions (and of foraging practices themselves) is thought to have further increased selective pressures for bigger brain and slower development (for an overview, see Dunbar & Schultz 2007).

5.1.2. Adaptive plasticity. As discussed earlier, humans as a species have a recognizable life history strategy, and show a distinctive pattern of life history traits. However, as in most species, there is also room for substantial variation between individuals. While some of this variation (e.g., in timing of maturation and reproduction) is heritable, organisms are also expected to embody mechanisms that evaluate the current (and expected) state of the environment and adjust their life history traits accordingly. In other words, life histories show *adaptive plasticity*. Mathematical models clearly show that the concept of a single "best" strategy is an illusion: what is expected (and found) is a variety of strategies, contingent on local conditions. The best strategy in a safe, predictable environment does not work well in a threatening and unpredictable one; the aim of maximizing long-term fitness can be targeted effectively only by organisms capable of context-sensitive (or state-dependent) adjustment of life history decisions (Houston & McNamara 1999; McNamara & Houston 1996). As Chisholm (1999) puts it, in the realm of life histories, "contingency rules." The study of context sensitivity in life history decisions has always been one of the key research topics in evolutionary anthropology (e.g., Blurton Jones 1989; Borgerhoff Mulder 1989; Hill & Kaplan 1988; Low 2000; Mace 2000a).

The key assumption of life history models of attachment is that, in humans, attachment relationships in infancy and early childhood (the first 5–7 years) provide the child with crucial information about the safety and predictability of his/her local environment. In turn, childhood attachment patterns are thought to translate into different reproductive strategies,[2] involving different trade-offs between current and future reproductive investment, and between mating and parenting effort. Of course, there are many other factors involved in the development of relational and sexual styles, including heritable dispositions, attractiveness, cultural practices, and the local sex ratio. The link between environmental stress, attachment, and adult reproductive strategy is thus expected to be only probabilistic (Gangestad & Simpson 2000; Schmitt 2005a; see also sect. 6.4 for a more detailed discussion).

5.2. The Belsky, Steinberg, and Draper model

The first systematic attempt to reframe attachment theory from a life history perspective was made by Belsky, Steinberg, and Draper (Belsky et al. 1991), drawing on previous work by Draper and Harpending (1982) on the effects of father absence on children's behavioral development. Belsky et al. noted that, in stressful conditions, parenting style becomes harsher and less sensitive and marital discord increases, causing the child to experience chronic psychosocial stress and leading to insecure attachment patterns. Insecure children thus receive crucial (albeit indirect) information about their environment: that resources are scarce and unpredictable, that people cannot be trusted, and that mating relationships tend to be short and uncommitted. This should switch development towards a reproductive style based on opportunistic interpersonal orientation, early reproduction, and low parental investment (offspring quantity vs. quality). Secure attachment/low stress, on the other hand, should lead to delayed mating, high parental investment, and a trusting and reciprocally oriented attitude. The reproductive strategies following secure versus insecure attachment are thought to be implemented by a suite of covarying traits, both behavioral/psychological (e.g., interpersonal orientation, sexual style) and somatic (e.g., accelerated sexual maturation). The result would be an adaptive polymorphism, based on condition-sensitive, developmentally contingent variation in life-history-related traits.

The theory predicted that early relational stress (and, by extension, insecure attachment) would relate to earlier maturation, earlier age of intercourse, and a tendency to entertain short-term relationships with mates. Although there is as yet no longitudinal study using attachment security to predict later maturation and sexual style, the evidence on the effects of relational stress and parenting consistently supports the main predictions made by Belsky et al. (1991). Note, however, that the weight of heritable genetic effects in linking mating and parenting across generations has yet to be fully evaluated; for example, age at menarche is known to be substantially heritable, at least in industrialized societies (current estimates are in the .40 to .50 range; see Campbell & Udry 1995; Chasiotis et al. 1998; Comings et al. 2002; Kirk et al. 2001; Moffitt et al. 1992; Rowe 2000a; Treloar & Martin 1990). For reviews of the evidence on early stress and accelerated sexual maturation, see Chisholm et al. (2005a) and Ellis (2004; 2005). See also Chisholm et al. (2005b) for recent data on early first birth related to insecure attachment. Recently, two longitudinal studies further confirmed the effects of parent–child relationships on sexual maturation. Ellis and Essex (2007) found that low-quality investment and marital conflict predicted earlier pubertal development in girls, and earlier onset of adrenarche in both sexes (see sect. 7.2). Belsky et al. (2007b) found that negative parenting predicted earlier pubertal development, but only in girls. They also found a moderating effect of early temperament, with infants low in negative emotionality showing the opposite pattern (i.e., negative parenting predicted later development; the meaning of this finding is still unclear).

The first version of the Belsky, Steinberg, and Draper theory had two main limitations. First, it treated insecure attachment as a whole, without distinction between avoidant and ambivalent strategies. Second, it assumed that the same reproductive strategy would be optimal for both males and females – an assumption that was immediately criticized by Maccoby (1991). The issue of sex differences has never been fully addressed by the theory (as noted also by Simpson 1999), perhaps because of the lack of sex-related differences in published attachment research. On the other hand, Belsky (1999) provided an updated version of the model, specifically addressing the issue of possible differences between ambivalent and avoidant strategies. Belsky (1997a; 1999) argued that his original analysis (predicting low-investment, short-term mating) was in fact more relevant to avoidant attachment, which is associated with parental rejection and high-risk, unpredictable environments. Similarly, Kirkpatrick (1998) conceptualized adult dismissiveness as a male-biased, short-term reproductive strategy. The hypothesized link between avoidance and short-term mating style is well supported by research in adult attachment. Dismissing adults are consistently found to be more promiscuous and sexually unrestrained; they are less committed in romantic relationships, are more likely to be sexually coercive, and tend to avoid intimacy with partners (reviewed in Allen & Baucom 2004; Belsky 1999; Brassard et al. 2007; Feeney 1999; Gentzler & Kerns 2004). In apparent contrast with these data, Cooper, Shaver and Collins (1998) found that avoidant adolescents of both sexes were less likely than secure ones to ever have had intercourse. However, the categorical measure they employed is likely to have misclassified as avoidant many fearful adolescents, high in both anxiety and avoidance (see Bartholomew 1990). This possibility is consistent with the study by Gentzler and Kerns (2004), who found high avoidance and moderately high anxiety both in students reporting no intercourse and in those reporting early intercourse (before 15 years). Finally, Bogaert and Sadava (2002) found that avoidance and anxiety both correlated with earlier age of first intercourse in women, but not in men.

In contrast with avoidant attachment (associated with a behavioral profile of self-reliance, pseudo-maturity, and aggression with peers in childhood), the ambivalent pattern is characterized by dependency, exaggeration of need signalling, behavioral immaturity, and passivity in peer relations. Belsky (1997a; 1999) speculated that ambivalent attachment was likely to develop in a form of delayed, indirect reproductive strategy. He hypothesized that ambivalent children would tend not to reach autonomy from the family, rather becoming their parents' "helpers-at-the-nest," and enhancing their own inclusive fitness by helping to raise younger siblings. Belsky then suggested that, for this reason, ambivalent children should often be first-borns. Interestingly, a study by Vondra et al. (1999) lent some empirical support to this specific prediction: Infants who became ambivalent at 18 months were more likely to be firstborn (and male), whereas avoidant children were more often later-born. To date, however, there is very limited support for the "helper" hypothesis; the sexual style associated with adult anxious attachment is also more complex than the avoidant one. Preoccupied individuals eagerly look for intimate relationships, and (if males) describe themselves as less accepting of casual sex (see Allen & Baucom 2004; Belsky 1999; Brassard et al. 2007; Feeney 1999; Gentzler & Kerns 2004); however, they also experience intense and impulsive sexual attractions (Hazan & Shaver 1987) and report higher frequency of infidelity (Bogaert & Sadava 2002). They are also more likely than secures to engage in unwanted sex following relational pressures and in order to keep their partner close (Impett & Peplau 2002; Schachner & Shaver 2002). This behavioral pattern, though different from that of dismissing adults, can nevertheless result in early onset of reproduction and in a relational style characterized by multiple matings, especially in women. Indeed, attachment-anxious women (but not men) are likely to initiate sexual activity earlier in adolescence (Bogaert & Sadava 2002; Cooper et al. 1998; Gentzler & Kerns 2004); and in a study of sexual fantasies, it was found that, in women, attachment anxiety predicts both more "romance" and more "unrestricted-emotionless sex" content (Birnbaum 2007). In a recent study by Jackson and Kirkpatrick (2007), anxiety showed a weak negative correlation with short-term mating orientation, and virtually no correlation with long-term orientation; in contrast, avoidance was weakly and positively related to short-term orientation, but strongly and *negatively* related to long-term orientation.

5.3. The Chisholm model

Chisholm (1993; 1996; 1999), drawing on the model of Belsky et al., proposed a complex theory of condition-dependent reproductive development based on attachment security. In Chisholm's model, attachment experiences provide children with information about the availability, sensitivity, and responsivity of their future social relations (a *socioassay* of their local environment). In a narrower sense, Chisholm (1993) proposed that caregiving conditions are used as a proxy for a critical life history parameter: the local mortality rate. This should lead to (unconscious) estimates of one's own expected lifespan and of the probability that one's offspring will survive, orienting towards earlier reproduction and higher mating efforts in the case of a risky environment. In addition, reproducing at a younger age means having fewer social resources (e.g., status, support networks) and, as a consequence, being less able to "make a difference" in offspring's quality; thus, early reproduction would further push reproductive strategies towards offspring quantity (vs. quality) and high reproductive rate. Intriguingly, there is evidence that insecurely attached adults tend to make shorter estimates of their own life expectancy (see Chisholm et al. 2005b), and that local mortality rates do correlate with familial environments and fertility patterns (Bereczkei & Csanaky 2001). In Chisholm's words, parents act as "vectors" through which the risk and uncertainty of the environment is transferred to children. Recent cross-cultural analyses by Quinlan (2007; Quinlan & Quinlan 2007b) strongly support the link between extrinsic risk factors (famine, warfare, and pathogens) and lower parental (especially maternal) investment. Furthermore, they suggest that unresponsive parenting and its developmental consequences (mating-oriented, risk-taking strategies) can influence cultural patterns related to casual sex, aggression, theft, and social hostility, thus contributing to a self-sustaining "culture of risk".

While it is predicted that both avoidant and ambivalent children will adopt life history strategies maximizing current reproductive effort, the two attachment strategies are thought to respond to different safety threats. In the case of parents who are willing, but unable to consistently invest in offspring, for example, because of scarce resources or competing demands on parents' time, the ambivalent strategy maximizes the available investment by increasing signals of need and behaving immaturely. When parents are unwilling to invest, however, the avoidant strategy is favored, pushing towards self-reliance and protecting the child from being abandoned or abused (Chisholm 1996). When insecure children grow up, they are expected to engage in low-commitment mating and low-investment parenting. Based on sexual selection theory (see further on), the model then describes two sex-specific developmental pathways leading to maximization of current reproduction (Chisholm 1999). Males growing in high-risk environments should adopt a strategy based on increased sex drive, aggression, impulsivity, and risk-taking, given the evocative label of Young Male Syndrome (from Wilson & Daly 1985). Insecure females should mature quickly as well, and their strategy should be characterized by impulsive mate choice (based on mate's genetic quality and immediate benefits), early and frequent childbearing, and single motherhood: the Young Female Syndrome. Of course, the two strategies represent the ends of a graded continuum, rather than being all-or-none choices.

What, then, about adult attachment styles? In Chisholm's model, ambivalent and avoidant insecure patterns are differently tuned to safety threats in the caregiving environment, but have no special role after reaching reproductive maturity. It would then make sense to think of attachment styles as ontogenetic adaptations – disposable phenotypes which have no reproductive value outside the caregiving environment. This contrasts with the empirical observation that insecure adults differ considerably in attachment styles, with measurable consequences for sexual and caretaking behavior. This is the main point of divergence from Belsky's revised theory; however, neither model succeeds in fully taking into account the different adaptive consequences of a given attachment pattern for males and females.

5.4. Some theoretical refinements

5.4.1. Environmental stability and "child development theory." A somewhat problematic assumption in life history models of attachment is that of substantial environmental stability in the time span from early childhood to puberty. In fact, only if ecological conditions are relatively stable is it adaptive for the child to set his or her future reproductive behavior according to current indices of mortality and risk (for a critique of this assumption, see Rowe 2000a). It is not clear to what degree ecological conditions have been (relatively) stable or fluctuating over our evolutionary history; nevertheless, the possibility of environmental fluctuations certainly reduces the reliability of parental behavior as a cue for expected risk. Belsky (2005) has suggested that cross-generational instability in environmental conditions could select for genotypic diversification in sensitivity to rearing influences, with some infants being genetically predisposed to be less affected by parental behavior than others (see also sect. 6.4).

In a discussion of parental effects on pubertal timing, Ellis (2004) proposed a new explanation of why low-quality parenting should accelerate the onset of puberty, which he labelled the "child development theory." The key idea is that children are not choosing their future reproductive strategy; rather, they are using information about parental investment in order to regulate the length of childhood. In this framework, the child is not responding to indirect macro-ecological cues (such as mortality), but to direct micro-ecological cues about his or her own rearing environment. If parental care is of high quality, the child can benefit by prolonging childhood and maximizing parental investment (e.g., food, wealth, skills teaching, status). If, on the other hand, parental investment is hard to come by, it might pay to shorten childhood and reach independence from parents at an earlier age. Child development theory is not incompatible with ecological risk models; in fact, it could help explain why some decisions concerning reproductive strategies are made so early in ontogeny, and disentangle the macro- and micro-ecological levels that make up a child's environment (see also sect. 7.1.1). Moreover, it is consistent with recent data on the anticipation of adrenarche (sect. 7.2). In section 6, I argue that an additional reason for early strategy switching is the importance of sexually selected traits in the context of children's peer relationships.

5.4.2. Attachment to mother and to father: Do they provide different cues? Although the models reviewed here focus on attachment security as a cue of ecological risk (and, in child development theory, of the future quality of parental investment), a whole literature inspired by Draper and Harpending (1982) has singled out paternal investment (and, in particular, father absence) as a crucial factor influencing pubertal timing in daughters (see Ellis 2004, for a review). The theoretical basis for focusing on paternal investment is that paternal care, much more than maternal care, is contingent on the mating system (monogamy vs. polygyny) and on the degree of local male–male competition for status, in addition to environmental risk (see also sect. 6.2). Thus, inconsistent or detached paternal care would act as a cue that (1) mating is polygynous (Kanazawa 2001), and/or that (2) paternal investment is unreliable, is probably not crucial for successful reproduction, and should not be expected from future partners. This would prompt daughters to adopt a reproductive strategy based on early sexual maturation (which is advantageous for females in polygynous systems; see Kanazawa 2001) and low commitment in long-term relationships (since paternal investment is not forthcoming). On the male side, sons from father-absent families tend to show increased aggressiveness and hypermasculine behavior (Draper & Harpending 1982), which can be seen as preparation for increased male–male competition for status (the Young Male Syndrome). Consistent with the idea of the father as a vector of mating-related cues, there is also evidence that harsh or insensitive fathering has a distinctive role in predicting the onset of "conduct disorder" in boys (reviewed in DeKlyen et al. 1999).

This suggests that security of attachment to mother and father may have different (and partly independent) effects on the development of boys and girls. Unfortunately, research on the developmental correlates of maternal versus paternal attachment is still carried out with virtually no reference to evolutionary hypotheses, so that the dependent variables employed in most studies lack direct biological relevance to male–male competition, status-seeking, and sexual style. Nevertheless, there is some interesting (if inconclusive) evidence of parent-specific effects: maternal attachment better predicts scholastic skills and "emotional maturity" in adolescence (Aviezer et al. 2002), a range of measures related to play quality and interpersonal conflict resolution (Suess et al. 1992), and "positiveness of self" in preschoolers (Verschueren & Marcoen 1999). On the other hand, paternal attachment, sensitivity, and availability seem to be more related to anxious/withdrawn behavior in preschoolers (Verschueren & Marcoen 1999), aggression with peers and peer rejection in middle childhood (Booth-Laforce et al. 2006; Verschueren & Marcoen

2002), and friend support, depression, and conflict with friends in early adolescence (Lieberman et al. 1999; Ducharme et al. 2002; Liu 2007). Most studies found no significant interaction with children's sex, but this may often depend on small sample size.

6. Sexual selection, parental investment, and sex differences in optimal life histories

6.1. Sex-specific life history strategies

Sexual selection (see Andersson 1994; Geary 1998; 2002) is, simply stated, natural selection following from the behavioral correlates of sexual reproduction. A character can be sexually selected in two main cases: when it is involved in same-sex competition for access to mates (intrasexual competition), and/or when it is related to mate choice by the opposite sex (intersexual choice). At a deeper level, the dynamics of sexual selection are driven by sex asymmetries in reproduction, especially those concerning parental investment (Clutton-Brock 1991; Trivers 1972). Members of one sex, usually females, provide higher investment in offspring production, both energetically and in parenting behavior; members of the other sex (usually males) invest less, and sometimes considerably less. In some species, this can consist of just the provision of sperm to females. As a result, the investing sex becomes the "choosing" side, while the other sex engages in strenuous competition for mates.

Sexual selection and asymmetries in parental investment are intimately related to the shaping of life histories (Höglund & Sheldon 1998; Kokko 1997; Svensson & Sheldon 1998). Life history strategies are essentially centered on achieving maximal reproductive success, and the way to attain the latter usually differs between males and females. As a consequence, males and females within a species experience different constraints, costs, and benefits, resulting in sex-specific life history strategies. The primary sex difference is in the balance of mating versus parenting effort (see sect. 5.1), with females investing more in parenting and males spending more time and energy in finding mates. This results from the fact that males enjoy higher maximum reproductive rates (i.e., potentially, a male can reproduce much more often than a female), so their benefit in pursuing additional matings can be much higher than it is for females. In addition, because males engage in same-sex competition, they usually need more developmental time and effort than females to reach an optimal degree of competitive ability. This is obviously true for physical size and strength, but it applies just as well to other sexually selected traits: Fighting ability, social competence, and courting displays all take time and energy to develop, as do the resources and social status needed for successful competition in humans. As a result, males tend to be slow developers and typically reach maturity later than females (Ellison 2001; Geary 2002).

6.2. Human reproductive ecology

What about humans? Most of the above applies to our species as well: Women invest more in offspring than men, and men show much of the standard repertoire of aggressive and status-oriented competition. Moreover, men develop more slowly than women, and tend to marry at a later age in most cultures (Eibl-Eibesfeldt 1989; Ellison 2001; Geary 1998; 2002; Mace 2000b). In addition, human reproduction features two important characteristics that, without being unique to our species, contribute to define the evolutionary landscape of sex-specific life histories: facultative paternal care and cooperative breeding.

6.2.1. Facultative paternal care. Human fathers participate in parental care of their children, sometimes rivaling mothers in the amount of investment they provide. This attenuates the asymmetry between the choosing and the chosen sex, and leads to female–female sexual competition and increased mate choice by males. However, paternal investment in humans is not an obligate trait: some men invest more and help mothers considerably, whereas others look for short-term mating opportunities and invest less in parenting (if at all). Such variation arises both between and within cultures, so paternal care in humans is best characterized as a facultative adaptation (see Geary 2005a; Hrdy 2005a; Miller 1994).

The degree of paternal investment found in a given population is determined by many factors; for example, paternal investment is expected to be enhanced if the fitness advantage conferred on offspring by the father's presence is substantial, if the opportunity for new matings is low, and if paternity certainty is high (see Geary 2005a). Availability of new mates stands out as an especially powerful factor: A survey of four hunter-gatherer societies by Blurton Jones et al. (2000) showed that mating opportunity (expressed as a function of fertile women-to-men ratio) was the strongest negative predictor of marital stability, which in turn is a major determinant of continued paternal investment across cultures (e.g., Betzig 1989; Draper 1989; Furstenberg & Nord 1985; Furstenberg et al. 1983). More generally, "father-absent" societies are characterized by aloof couple relationships, polygyny, warfare, and high levels of male competitive displays. This pattern is often seen in resource-rich ecologies, and in societies practicing low-level agriculture (Draper & Harpending 1988). A cross-cultural study by Quinlan (2007) showed that paternal and maternal care respond differently to environmental risk: Whereas maternal care decreased steadily with increasing famine and warfare, and with high levels of pathogen stress (while increasing at moderate levels), paternal involvement was negatively related to pathogen stress, and only weakly related to famine. Moreover, the local degree of polygyny seemed to partly mediate the association between pathogen stress and paternal involvement. Polygyny is strongly predicted by high pathogen stress (Marlowe 2003), so in general it may covary with extrinsic risk and mediate its effects on paternal care. In polygynous societies, males contribute less to subsistence, and direct paternal care is reduced (see also Marlowe 2000; 2003); counterintuitively, couple stability is increased overall, probably due to the shortage of women created by polygyny (Quinlan & Quinlan 2007a) and to the fact that polygynous men need not divorce and remarry if they can afford to acquire new wives (Marlowe 2000). Couple stability, however, can well coexist with high mating effort, as shown by the lower investment in paternal care and the increased frequency of extramarital affairs in polygynous/low male provision societies (Marlowe 2000).

6.2.2. Cooperative breeding and alloparental care. The second characteristic is that humans, like a small number of other primates, probably have an evolutionary history of cooperative breeding (Hrdy 1999; 2005a; 2005b; Kramer 2005; Mace & Sear 2005). Mothers living in ancestral groups were not alone in caring for their children, but could elicit *alloparental care* from others, especially older children and female relatives (i.e., grandmothers and aunts). The presence of maternal grandmothers and older sisters has been shown to increase child survival in many populations, with smaller but similar effects for maternal grandfathers and older brothers (reviewed in Mace & Sear 2005).

Cooperative breeding has been documented in many traditional societies, and shows remarkable cross-cultural invariance. In a survey of traditional cultures by Kramer (2005), infants received about 50% of their daily care time from mothers, with little variation in percentage between cultures; the remaining 50% was distributed among siblings (10–33%), grandmothers (1–12%), other alloparents (3–21%), and fathers. Fathers' contribution to direct infant care was rather variable and, one would say, not very impressive, ranging from less than 1% to about 6% of time. Similar figures are found in nontraditional societies as well (e.g., Geary 2000; Lamb et al. 1982: Lampert & Friedman 1992). Note that I am not equating paternal investment with direct caring time; paternal investment in humans comes in many forms, including food provision, protection, teaching, and social status (Geary 2000; Geary & Flinn 2001). However, these data strongly underline the importance of alloparenting in human reproductive ecology.

Hrdy (1999; 2005a; 2005b) argued that, as happens in other cooperatively breeding primates, human mothers without available alloparents (partly synonymous with "social support") are more likely to abandon, neglect, or even kill their children (see also Hill & Hurtado 1996; Wasser & Barash 1983). If alloparental care is really so vital for human mothers, its absence (or low quality) should be considered a specific, major source of environmental stress; for females, the "socioassay" taken in the first 5–7 years of life should definitely include the availability of alloparents, including one's own parents and siblings. The evolutionary importance of cooperative breeding would also explain the tendency of young children to form multiple attachments, while at the same time maintaining a "special" relationship with a primary attachment figure (usually the mother) – a phenomenon labeled monotropy (see Ahnert 2005; Cassidy 1999).

6.3. Implications for attachment theory

Because of asymmetries in parental investment and sexual selection, males and females face different trade-offs in their life history decisions. This must be taken into account by life history models of attachment, and related to expected costs and benefits of different strategies. Chisholm (1999) described sex-specific reproductive strategies under the labels of Young Male and Young Female Syndrome (sect. 5.3); in this section, I extend his analysis and those of Belsky (1999) and Kirkpatrick (1998) by considering how sex-specific selective pressures and trade-offs might relate to insecure attachment styles.

6.3.1. Sex differences in the mating versus parenting balance. Current life history models link insecure attachment to a developmental trajectory of early reproduction, low commitment in long-term couple relationships, and low parental investment. However, from the above discussion, it is apparent that low parental investment involves different cost/benefit ratios for males and females. Males, much more than females, are facultative investors: for a male, low parental investment can be a very effective strategy, especially if the costs of raising a child are borne by the mother and her alloparental network. Moreover, uncertainty of paternity lowers the benefits of investing in one's (probable) offspring. The decrease in fitness following lower investment in already-born children can be compensated for by additional matings; thus, males are able (in certain conditions) to employ a zero-parenting strategy wherein virtually all resources are devoted to mating. For women, such an extreme low-investment strategy is not feasible, since they are usually the primary caregivers and infants need at least some basic parental investment to survive. Even more crucially, women's fitness does not benefit as much from mating with additional partners, given the strong limitations on female maximum reproductive rate. In other words, women cannot shift the balance between parenting and mating effort as easily as men (Archer & Mehdikhani 2000).

In conditions of heightened environmental risk, both males and females are expected to adopt reproductive strategies focused on current reproduction and increased mating effort at the expense of parenting. However, the strategic balance in resource allocation will differ between the sexes, with males engaging in lower levels of parental effort than females. With increasing risk, the optimal investment for males will fall off rapidly because, when approaching the "saturation point" of offspring fitness, parental effort has diminishing returns (sect. 5.1), and the resources needed to increase offspring quality by a small amount can bring higher benefits if successfully diverted to mating. This is not the case for females, who cannot increase their reproductive output beyond a certain amount, nor avoid the basic (but by no means trivial) investment of pregnancy and lactation. Females will then favor a higher level of parental investment in each offspring, and are thus expected to (1) invest more than males in parental effort, and (2) try to elicit additional investment from mates and/or alloparents. Only at high levels of risk (i.e., when the saturation point becomes very low), can females meet the optimal investment even with little or no contribution from mates and/or alloparents.[3] Then, at high levels of risk, females are expected to engage in low-investment mating without demanding additional investment. On the contrary, when the environment is safe (high saturation point), the optimal level of parental investment can become very high, and both males and females can gain by investing considerably in parental effort, thus maximizing offspring quality and their own long-term fitness. However, even at low levels of risk, paternal linvestment is more contingent on the degree of polygyny and on the availability of new partners, which can considerably increase the benefit of diverting some resources from parenting to mating.

Although increasing risk generally favors quantity-oriented strategies, scarcity of social resources in absence of elevated risk could instead favor reproductive suppression (i.e., delaying reproduction until resources become available) in females (Wasser & Barash 1983). The same happens when energetic resources are scarce, which delays maturation and, in mature females, induces temporary suppression of fertility (see Ellison 2001; Ellis 2004). I suggest that lack of available alloparents (including potential mates) might lead to temporary reproductive suppression in women who are not adopting a low-investment strategy; this may involve behavioral correlates such as reduced sexual motivation and/or reduced interest in couple relationships (either long- or short-term). While this suggestion is openly speculative, it is crucial to keep resource scarcity as distinct as possible from environmental risk, since the two are expected to exert different effects on reproductive strategies (see also Clark & Daly 2005).

Translating the above considerations into the framework of attachment theory, insecure males should readily adopt avoidant strategies, which are most likely to maximize their fitness in a threatening environment. Insecure females, on the other hand, should preferentially adopt anxious, care-eliciting strategies (i.e., preoccupied/ambivalent attachment). This would keep them in close contact with kin, and help spread the costs of reproduction onto relatives. In cooperative breeding systems, the "helper" strategy can coexist with the helper's own reproduction (Clutton-Brock 2002); thus, Belsky's hypothesis about ambivalent attachment as helping-at-the-nest (sect. 5.2) could be partly correct, although without involving delayed reproduction. Maximizing help from kin is not the only benefit of anxious attachment: In the context of couple relationships, anxious behaviors (e.g., dependence, preoccupation with intimacy and partner availability) can help to maintain closeness with one's partner, especially if the latter is avoidantly attached, and to maximize the available paternal investment (thus enacting a sort of "counter-strategy" to male avoidance). Intriguingly, an early study by Kirkpatrick and Davis (1994) found that couples made up of dismissing men and preoccupied women can be long-lasting, as much as the secure-secure ones (even while enjoying less couple satisfaction). There is also evidence that preoccupied women find it especially difficult to end couple relationships, even following abuse or deceit by their partner (Henderson et al. 1997; Jang et al. 2002). This is consistent with a strategy aimed at maximizing closeness and continued investment, even by reluctant or uncommitted mates. Thus, in the context of cooperative breeding, the anxious phenotype can be a useful device for adult females to extract investment and care from both relatives and mates. In this framework, females are expected to adopt male-like avoidant strategies as a second choice, tailored to high levels of environmental risk. This view is supported by the cross-cultural survey by Schmitt et al. (2003a), who found dismissiveness in women to covary with environmental risk and mortality rates, and to do so much more strongly than in males (on average, $r = .40$ versus $r = .23$). Finally, scarcity of social resources (in absence of high risk) can be expected to induce temporary reproductive suppression in females. This possibility has not been yet considered in evolutionary models of attachment, but (if supported by evidence) it would have important implications. For example, some avoidant women may be actually adopting a temporary suppression strategy (e.g., by avoiding sexual relationships altogether), and shift to anxious or secure patterns when social conditions improve; even if suppression was not related to specific attachment patterns, it could alter the expected relationship between attachment and sexual behavior.

The idea that women's reproductive strategies are highly condition-sensitive is not new and has been championed by Lancaster (1989) and Hrdy (1999; 2000). Basically, they contend that, when monogamy is not a viable choice (e.g., because of low paternal investment and/or low quality of potential mates), women can adopt "facultative polyandry" as their optimal strategy. Mating with many partners allows the exchange of sexual access for immediate benefits and, even more importantly, creates a network of "possible fathers," who can then provide protection and help, and be tolerant (non-aggressive) towards the mother's children. The theory I propose is compatible with the facultative polyandry hypothesis, while adding another layer of complexity to female strategies. Avoidant strategies can easily lead to polyandry; for reasons discussed earlier (sect. 5.2), anxious strategies can lead to multiple matings as well, while retaining an orientation to long-term commitment. Finally, some women may be actually adopting a third kind of strategy – one aimed at temporarily suppressing reproduction because of scarcity of available alloparenting and social support.

6.3.2. Intrasexual competition. There is one more reason to consider attachment in the light of sexual selection: Because attachment patterns are related to the development of personality traits (and, in general, exert a powerful organizational effect on social development), their costs and benefits should differ between males and females if the traits in question are sexually selected. Avoidant attachment, which is related to inflated self-esteem (Cassidy 1988) and aggression with peers (e.g., Card & Hodges 2003; Erickson et al. 1985; Finnegan et al. 1996; Renken et al. 1989), is likely to be more adaptive for young males who need to defend their social status in anticipation of early reproduction (male–male competition); moreover, the above-mentioned traits can be attractive to females, thus contributing to mate choice (see Sadalla et al. 1987; Weisfeld et al. 1983).

The opposite applies to ambivalent attachment, which predicts fearfulness, withdrawal, and passive behavior with peers (e.g., Card & Hodges 2003; Cassidy 1988; Cassidy & Berlin 1994; Erickson et al. 1985). These traits are not nearly as damaging for females as they are for males. For example, Morison and Masten (1991) found that the "sensitive-isolated" behavioral profile in middle childhood was associated with lower self-worth in males, but higher self-worth in females. Also, studies correlating attachment with externalizing (e.g., aggression, disruptiveness) and internalizing (e.g., anxiety, withdrawal) behavioral problems often find effects that are sex-specific to some degree. In the study by Renken et al. (1989), avoidance predicted externalizing symptoms only in males; and Finnegan et al. (1996) found that avoidant coping was correlated with more externalizing problems, but fewer internalizing problems in males; preoccupied coping, on the other hand, was related to higher internalizing problems in males but not in females. Ambivalent children also tend to be victimized in peer groups, especially by avoidant children, who instead take the role of bullies (Troy & Sroufe 1987; Finnegan et al. 1996). Although bullying has traditionally been associated with peer rejection (e.g., Pellegrini 1995; Weisfeld 1999), being a bully is usually better than being a victim (e.g., Juvonen et al. 2003), and may be a reasonable way to secure one's place in male dominance hierarchies and gain access to social resources. Indeed, researchers are becoming increasingly aware that not all bullies are equal; especially among older children and young adolescents, there is a subgroup of aggressive children who are accorded high peer status, are rated as "cool" and attractive by girls, and date more often (e.g., Juvonen et al. 2003; Pellegrini & Bartini 2001; Rodkin et al. 2006). Whereas, in early childhood, aggression is associated with peer rejection (note, however, that rejection and dominance status are only weakly correlated), at later ages it becomes increasingly predictive of peer acceptance (Bukowski et al. 2000).

In synthesis, the overtly aggressive and self-aggrandizing style of avoidant children can provide a competitive way to gain status and dominance in male groups. The ambivalent pattern has been less studied, because of its relatively low frequency in early childhood, so it is more difficult to relate it to possible adaptive benefits for girls (at the same time, we know less about the mechanisms of dominance and status in female peer groups). What has been observed empirically is that insecure patterns are more extremely skewed in boys than in girls, and it is then possible that intrasexual competition has stronger implications for male attachment as well.

6.3.3. Why middle childhood? Middle childhood (approx. age 7–11 years) is the human homologue of the primate juvenile phase. Children of this age, like other juvenile primates, no longer depend exclusively on parental care for survival, and can forage effectively if they need to do so. At the same time, they are still sexually immature and have limited competitive abilities (see Bogin 1999; Geary & Bjorklund 2000; Kramer 2005). In this developmental phase, the peer group becomes the child's primary interpersonal world; fight play, parenting play, and same-sex grouping all peak between 6 and 11 years of age, with little cultural variation (e.g. Geary 1998; 2002; Serbin et al. 1993).

Conventional wisdom about children's peer interactions is that they allow for "safe experimentation" with adult social skills. However, childhood peer relationships also have lasting effects on people's lives, much more so than is usually realized. For example, dominance ranks in childhood tend to carry over into adolescence: In a longitudinal study by Weisfeld et al. (1987), "toughness" ranks of boys at 7 years of age correlated about .70 with dominance, popularity, and leadership at age 16. Other studies found stability from childhood to adolescence in related personality traits, such as dominance and passivity (reviewed in Weisfeld 1999). Although the influence of heritable traits on these results has not been quantified (social dominance is also related to strength and physical attractiveness, and shows moderate heritability; e.g., Gottesmann 1966), it seems reasonable to consider that early outcomes, especially in the field of dominance and status, can have a lasting influence on later development. "Social inertia" is a well-known phenomenon in animal dominance hierarchies: After the first encounters settle the initial ranking, individuals tend to keep their position in the hierarchy as long as they remain in the same group, even if their hormonal levels are experimentally manipulated to match those typical of higher-ranking animals. The same manipulations, however, have dramatic effects if an individual is placed in a new, unfamiliar group (Adkins-Regan 2005). Human juveniles are not just "preparing" for their adult roles; they are actually establishing a starting place in the social group, which in turn will influence their future reproductive opportunities to some degree. In this phase, conflict between early behavioral strategies (influenced by parental care) and new environmental demands (driven by the peer group) could start becoming apparent, to culminate later during adolescence.

6.4. Multiple factors affecting reproductive strategies

6.4.1. Other environmental factors. A cautionary note is warranted at this point. As mentioned above, individual reproductive strategies are not completely determined by developmental factors such as attachment security and early stress. Many researchers have argued for a multifactorial view of reproductive decisions, and have described other factors affecting mating strategies: local sex ratio, pathogen load, social and economic structure, self-perceived mate value, attractiveness, and age (see Barber 2000; Campbell 2000; Cashdan 1996; Gangestad & Simpson 2000; Landolt et al. 1995; Schmitt 2005a; Schmitt et al. 2003b; Voland 1998). Of course, some of these factors (e.g., sex ratio, pathogen load) are known to affect parental investment, and their effects could turn out to be partly or fully mediated by early stress and attachment; other factors (such as attractiveness and age), however, are likely to have independent effects on reproductive strategies.

For example, a cross-cultural study by Schmitt (2005a) found that, while low interpersonal trust and insecure attachment correlated with short-term mating, there were also many associations between short-term mating and "positive" traits, such as low psychological symptoms and high self-esteem – especially in males. In addition, short-term mating in men tended to increase with age, and men were on average more oriented to short-term mating, regardless of attachment style. Similar findings were reported by Egan and Angus (2004). They found that rate of sexual infidelity correlated positively with psychopathic traits (i.e., manipulative and egocentric behavior) and negatively with agreeableness and social desirability in both sexes; however, men who had been unfaithful at least once were higher in socially desirable personality traits such as agreeableness, extraversion, and conscientiousness. Clearly, these results support a multifactorial model of reproductive choices. Generally speaking, it must be stressed again that males have a bias towards short-term mating, probably because of the high benefit/cost ratio of this behavioral option (e.g., Buss & Schmitt 1993; Schmitt et al. 2003b); highly attractive men may actually look for an increased number of short-term partners (Gangestad & Simpson 2000; Jackson & Kirkpatrick 2007; Landolt et al. 1995). Schmitt (2005a) also found a tendency for short-term mating orientation to increase in people either living with a partner or married, making it clear that commitment in a long-term relationship and high parental investment can coexist with the occasional pursuit of short-term mating opportunities (see also Geary 1998).

6.4.2. Heritable individual differences. Individual differences in reproductive strategies are also affected by heritable genetic variation. In section 5, I mentioned findings of substantial genotypic variance in life history traits, such as pubertal maturation and age at menarche. Other researchers have tried to investigate the broader spectrum of life history strategies, and they also found support for the idea that heritable factors play an important role in shaping human reproductive styles. Figueredo et al. (2006) summarized their research on the "K-factor,"[4] a global measure (derived by factor analysis) accounting for a large portion (about 70–90%) of reliable variance in a broad class of life-history-related traits (such as attachment to parents, romantic attachment security, mating effort, manipulativeness, risk-taking, and altruistic feelings). In a twin study, the heritability of the K-factor was estimated at .65 (Figueredo et al. 2004), suggesting considerable genotypic influence. As the authors note, the same result also implies that a substantial portion of variance in reproductive strategy is influenced by environmental factors (and/or genotype-environment interactions).

A common evolutionary explanation of heritable individual differences in sexual strategies invokes the concept of frequency-dependent selection (e.g., Campbell 2000; Gangestad & Simpson 1990; Rowe et al. 1997). Genetic variation can be maintained if the resulting phenotypes are adaptive in the context of the other phenotypes present in the population. For example, if all males provided low parental investment and engaged in high competition, it could be adaptive for some of them to become less competitive and to invest more in parenting, so that genes favoring parental investment would spread; the two strategies might eventually reach an equilibrium state, each at its optimal frequency, and coexist in the population (note that more complex and "dynamical" outcomes are also possible; e.g., involving cycles in genotype frequencies). Nettle (2006; 2007) provides a good introduction to the possible sources of heritable variation in behavioral traits, including frequency-dependent selection.

The empirical data support the view that human reproductive strategies are shaped by both heritable and environmental factors, with the possibility of substantial gene–environment interaction (different genotypes showing different conditional responses to the environment). It is also possible that some genotypes are more responsive than others to environmental cues; this hypothesis of "differential susceptibility" to rearing environment was proposed by Belsky (1997b; 1999; 2005) in the context of early stress and attachment styles, and is gathering increasing empirical support in various domains (Belsky et al. 2007a).

7. A synthesis: Attachment and the development of reproductive strategies

I now draw upon theory and evidence presented up to this point, and outline an updated synthesis of the life-history model of attachment. First, I follow the main phases in the development of the attachment system, from infancy to adulthood (Fig. 2), highlighting the empirical predictions derived from the model at each stage. Then, I propose a hormonal basis for the middle childhood transition, discuss the evidence for the influence of sex hormones on attachment, and speculate on its implications for theory and research.

In dealing with insecure attachment patterns, I will focus on the avoidance/ambivalence dimensions, leaving aside the issue of disorganization. There are three pragmatic reasons for this choice: first, the literature on attachment and life histories has been mainly concerned with explaining avoidant and ambivalent patterns. Second, disorganization is in many ways orthogonal to the three-way (ABC) classification, and (especially if low to moderate) can coexist with a primary, organized pattern; thus, its effects are likely to interact with those of the avoidant/ambivalent components. Last and most important, adult attachment questionnaires do not assess disorganization or its sequelae, so that at present it is hard to track the disorganized developmental trajectory from childhood to adulthood (but see Simpson & Rholes 2002, for the interesting proposal that fearful-avoidant romantic patterns may reflect disorganization). That said, I have no intention of downplaying the importance of disorganized attachment, and investigating this issue will be a crucial task for future research and theoretical work. Disorganized attachment is often related to severe levels of psychosocial stress and is characterized by sex differences from early childhood – two features that suggest high relevance to the life-history model proposed here.

7.1. Developmental phases and transitions

7.1.1. Infancy and early childhood. In infancy and early childhood, the attachment system has the function of eliciting care and protection during the period of maximal dependence on parents. For this reason, attachment styles can be expected to track caregivers' behavior quite closely, adapting to changes in environmental and parenting conditions as shown by longitudinal studies. No strong sex differences in attachment patterns are predicted (nor have been reported) in this developmental phase; as an exception, males are more often and severely disorganized than females (sect. 4.1). At the same time, young children use attachment security as a "socioassay" of their current (and expected) local ecology. Insecure attachment acts as a cue that (1) the environment is risky, possibly involving high mortality rates, and/or (2) the child should expect to receive low parental investment in the future; this includes physical resources, teaching, protection, and alloparenting. As discussed in section 6.3, the presence and availability of alloparents (including siblings, other relatives, and potential mates) could be an important cue driving female reproductive strategies, and possibly influencing attachment security and/or style in girls.

The macro- and micro-ecological cues gathered in early childhood also affect the timing of the child's transition to juvenility (marked by adrenarche; see sects. 5.2 and 7.2). Child development theory (sect. 5.4.1) suggests that low-quality parental investment should lead to shortened childhood, as recently confirmed by Ellis and Essex (2007), who found that early stress anticipates adrenarche in both sexes. At the same time, insecure attachment acts

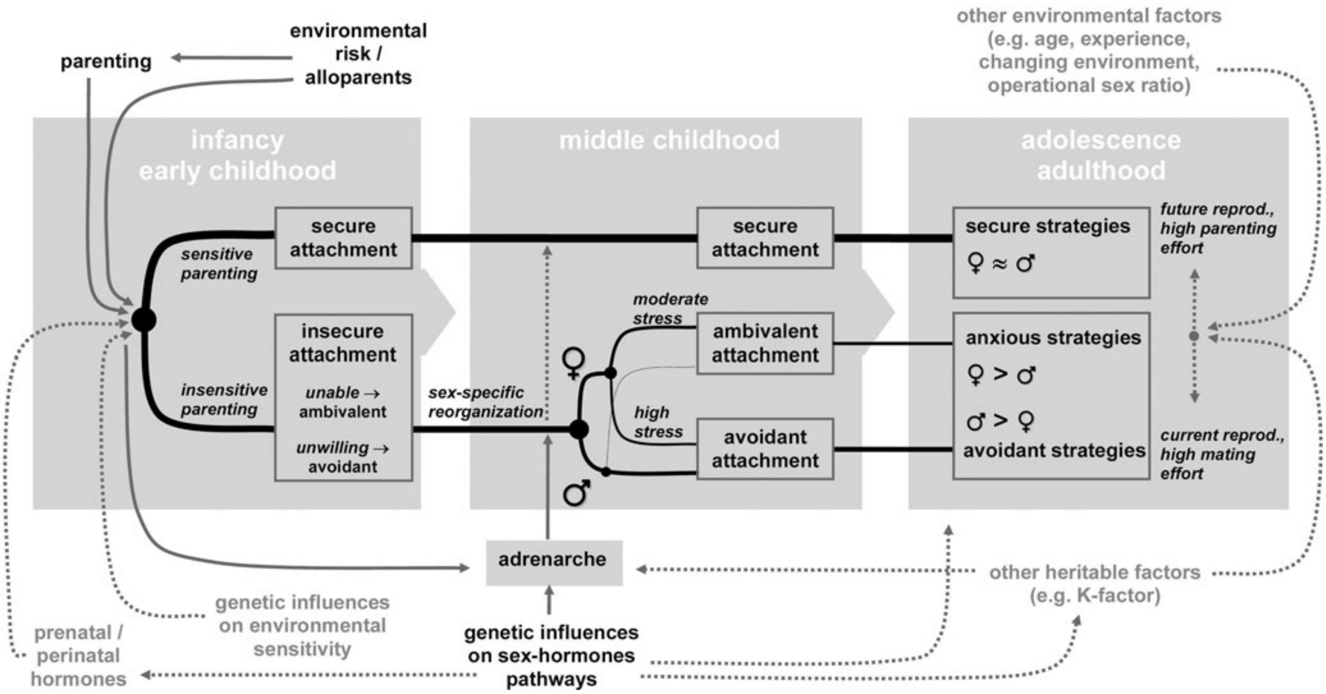

Figure 2. Schematic diagram of the development of reproductive strategies. Black lines represent typical developmental pathways, with thickness roughly proportional to phenotype frequency in relatively low-risk populations. The core causal relationships discussed in the text are indicated by solid arrows; dashed arrows represent other possible effects, relevant to the model but not discussed in detail here. For ease of presentation, the diagram shows high stability in attachment security across infancy and childhood. This is a simplification, as changes in security are possible throughout the lifespan. In addition, attachment strategies are depicted as discrete categories, although they are probably better described as continuous dimensions.

as a cue of environmental risk, thus leading to current reproduction-oriented life history strategies and earlier maturation. Note that low parental investment can act as a indication of risk for two reasons: it can inform the child that extrinsic risk is generally high, but it can also mean that parents are not willing to invest in that specific child for other reasons (e.g., low phenotypic quality, presence of step-parents, cultural bias against males or females, etc.), resulting in higher mortality risk for the child itself. Of course, the likelihood of such discrimination by parents will increase when social resources are scarce and/or ecological risk is high (see also Chisholm 1999). Thus, parental investment can act as a cue of risk at both the macro- and micro-ecological levels, which helps to explain why one finds variable degrees of attachment security within the same social group and the same family (another reason being genotypic variation in environmental susceptibility).

7.1.2. Middle childhood: A transitional phase. At the beginning of middle childhood, or human juvenile stage, the attachment system undergoes a phase of remarkable reorganization. The available data show that insecure children's attachment patterns become highly sex-biased, so as to switch their reproductive strategies towards sex-optimal developmental pathways. Attachment security/insecurity is a reliable index of socioecological risk, and, as such, it is retained as a relatively stable, prototype-like behavioral trait[5] (Fraley 2002). The specific insecure strategies adopted in early childhood, on the contrary, can be viewed as disposable phenotypes, to be modified during development if they do not suit the adaptive interest of the growing children (see sect. 3).

The most immediate selection pressure on attachment styles in middle childhood probably comes from intrasexual competition in the peer group (sect. 6.3.2). In middle childhood, children begin to fight their way through social reality, and the first outcomes can have long-lasting effects on future development – perhaps more so for insecure children, who cannot count on a protective family network to buffer them against difficulties and failures. Thus, the behavioral correlates of attachment patterns are likely to be sexually selected already at this stage. In particular, the avoidant pattern is associated with aggression, self-reliance, and inflated self-esteem – all traits that can be useful to males as a high-risk status-seeking strategy. Indeed, empirical studies in middle childhood show that nearly all insecure boys can be classified as avoidant. Girls, on the other hand, tend to shift to ambivalent styles (while in a less extreme fashion); it is less clear whether this particular pattern gives them some advantage in the peer group, or if it just anticipates adult strategies. Notably, attachment in middle childhood does not relate only to aggression: Sroufe and colleagues (1993) found that insecure children aged 10–11 years were more likely than secure ones to "violate gender boundaries," which included flirting, physical contact, and sexual gestures. This is fully consistent with life-history models, and indicates that insecure strategies may relate to earlier initiation of sexual activity already in middle childhood.

A question may arise at this point: If avoidant attachment can be such a rewarding strategy for males, why don't all males (including secure ones) shift to this pattern? In fact, there is evidence that, among secure boys, a sizeable proportion shows secondary elements of avoidance (sect. 4.2;

Del Giudice 2008), so this could be partly correct. However, it is not the case that successful social strategies always involve competitive status-seeking. If environmental conditions are safe and predictable, and if the local mating system favors monogamy and high paternal investment, then low-risk, cooperative strategies can be more successful in maximizing males' long-term fitness (sect. 6.3.1); lower male avoidance is predicted in this case, consistent with weaker male-male competition and reduced conflict of interest between mothers and fathers.

As mentioned in section 5.4.2, it is possible that maternal and paternal attachment play different roles in determining the behavioral strategy adopted in middle childhood. Maternal and paternal investment seem to respond differently to extrinsic risk (Quinlan 2007; see sect. 6.3.1), and could, therefore, be expected to shape children's life history strategies in somewhat different ways. In particular, paternal investment can carry useful information about the local degree of male–male competition, polygyny, and paternal involvement, which could affect specific aspects of children's attachment and behavior (e.g., competitiveness and risk-taking in boys, avoidance vs. ambivalence in girls). Further research is needed to assess the merit of this hypothesis, and to make sharper predictions about the possible effects of maternal versus paternal attachment on sons and daughters.

Finally, although attachment-based models focus on environmental cueing of secure versus insecure and avoidant versus ambivalent strategies, heritable effects are also likely to influence development in this phase. As I explain in section 7.2, the physiological changes taking place in middle childhood are likely to reveal previously unexpressed genotypic variability, which could significantly affect the regulation of life-history-related traits (including attachment). In fact, heritable effects on adult romantic attachment styles have been recently found using the RSQ (Brussoni et al. 2000); no comparable study has been yet performed in middle childhood. Genotypic variation can affect reproductive strategies in many ways; one possibility is that the genotype influences the degree of environmental sensitivity, leading to relatively flexible versus fixed strategies, as proposed by Belsky (2000; 2005; Belsky et al. 2007a).

7.1.3. Adolescence and adulthood. With the coming of adolescence, the attachment system finally takes on its mature function, that of regulating couple relationships and mating strategies. In general, insecure strategies can be seen as maximizing current reproductive success and privileging mating effort at the expense of parenting. However, the mating versus parenting balance entails different trade-offs for males and females (sect. 6.3.1). Insecure males are predicted to favor avoidant strategies (low parental investment, short-term and uncommitted mating), whereas insecure females are expected to show a broader range of phenotypes: they should adopt anxious, investment-eliciting strategies when environmental risk is moderate, and avoidant strategies when faced with challenging conditions. Both strategies are usually related to impulsive mating and to short-term sexual orientation in females; however, whereas avoidant women show little desire for commitment and intimacy, anxious women also show heightened desire for long-term relationships, intimacy, and romance (sect. 5.2). Female anxiety could partly act as a "counter-strategy" to male avoidance, by coupling impulsive mating (which can initially attract avoidant males) with high requests for commitment and investment. To render the picture more complex, some women may adopt a temporary strategy of reproductive suppression, possibly marked by low interest in both short- and long-term relationships, due to perceived lack of social resources. Finally, secure adolescents of both sexes are expected to follow parenting-oriented reproductive strategies maximizing future reproduction (later onset of reproduction, high commitment in couple relationships, high parental investment, and later puberty in girls).

In the present model, avoidant/ambivalent patterns after the middle childhood transition are expected to predict avoidant/anxious attachment strategies in adulthood. This would provide a developmental basis for adult measures of romantic attachment, which to date lack a clear theoretical and empirical link to childhood antecedents (Belsky 2002). A related prediction is that the size of sex differences in middle childhood should mirror that in the adult population. One should find larger differences in cultural regions characterized by moderate environmental risk, somewhat smaller differences in low-risk regions (because of higher security in both sexes), and the smallest differences (mostly driven by higher female avoidance) in high-risk regions. It is noteworthy that, until now, reports of marked sex differences in middle childhood all came from regions showing above-average adult sex differences in the cross-cultural study by Schmitt et al. (2003a): Italy ($d = .21$), Israel ($d = .21$), western United States ($d = .26$), and Canada ($d = .35$).

To end this section, I briefly turn to the issue of plasticity in adulthood. Current life-history models tend to confine plasticity to the first years of life, without considering how individuals may adjust their strategies later in development. Nevertheless, it is quite reasonable to assume that, given the long reproductive lifespan of humans, there is room for strategic change in adolescence and adulthood as well. Improvements in social support and in the quality of couple relationship are known to affect parenting and attachment, as noted by Chisholm (1993; 1999); ultimately, changing socioecological contexts could lead adults to "revise" their reproductive strategies, with behavioral as well as physiological consequences (see also Cashdan 1996). Age itself is a key variable affecting the main life history trade-offs, with likely consequences for mating and parenting strategies (e.g., Delton et al. 2006). For example, males throughout the world tend to shift from high mating effort in young adulthood to a phase of increased parental investment (Winking et al. 2007); this transition may be especially dramatic in insecurely attached men. In section 4.3, I reported initial evidence that sex differences in attachment styles peak in late adolescence and decline towards middle age; this supports the idea that sexual selection on reproductive strategies is stronger in early adulthood, and that the relational styles of men and women become substantially more similar at later ages. Finally, researchers are beginning to study how attachment representations change following marriage and parenthood (e.g., Crowell et al. 2002; Treboux et al. 2004); results from this research field will be extremely useful in increasing the realism of life-history models.

7.2. Hormonal basis of the middle childhood transition

So far, I have argued that middle childhood is an important transitional period, and have provided the evolutionary rationale to support this view. However, the idea that behavioral change at this age is related to sexually selected strategies may sound strange, since this kind of transition is usually associated with the later onset of puberty. On the biological side, middle childhood appears to be characterized by stasis rather than change – perhaps a legacy of the Freudian concept of "latency." This view is incorrect. On the contrary, middle childhood is a phase of intense (though physically concealed) endocrine development, anticipating puberty in many respects. As I show in this section, there are reasons to consider middle childhood as the actual beginning of "adult" sexual differentiation at the neurobehavioral level. The possibility that sex differences in attachment styles (precursors of reproductive strategies) are primed by such hormonal changes should definitely be considered and investigated.

7.2.1. Adrenarche. At about 6 years of age, with little difference in timing between males and females, the adrenal cortex of both sexes begins to secrete a growing amount of androgens into the bloodstream. These do not include the familiar androgen testosterone, which will begin to rise later in puberty. The main products of adrenal glands are dehydroepiandrosterone (DHEA), dehydroepiandrosterone sulfate (DHEAS), and androstenedione (A4), three chemical precursors of testosterone and estrogen. Secretion of adrenal androgens increases steadily for about 10 years, reaches a peak in early adulthood, and then slowly declines. The onset of adrenal androgen production is called adrenarche, and marks the beginning of the developmental phase known as adrenal puberty (Auchus & Rainey 2004; Ibáñez et al. 2000; Palmert et al. 2001; Spear 2000).

Adrenal puberty is a peculiar feature of human development, absent in most other mammalian species (including primates); to date, it has only been documented in chimpanzees and gorillas, which also undergo a prolonged juvenile phase before reproduction (Ibáñez et al. 2000). DHEA and DHEAS were once thought to be "weak" androgens, because they show low affinity with androgen receptors, and as such were largely ignored by researchers. However, it has been recently discovered that brain cells (and other peripheral tissues) express the enzymes needed to convert precursors such as DHEA into "active" testosterone and/or estrogens (see Adkins-Regan 2005; Labrie et al. 2005). According to current estimates, such "intracrine" production of sex hormones in peripheral tissues accounts for about 75% of total estrogen in women and 50% of total androgens in men (Labrie et al. 2005). Thus, adrenal androgens contribute significantly to sex-hormone production in adults; in children, they can drive development along sex-specific developmental pathways before full reproductive maturity.

Through local conversion to testosterone and estrogen, adrenal androgens can be behaviorally active even if they have only minimal effect on bodily development (i.e., initial growth of axillary and pubic hair, increased oil in the skin, and a slight acceleration of skeletal growth). They may also exert direct behavioral effects, via neuromodulation of GABA receptors and upregulation of the androgen receptor (see Simon & Lu 2006). Indeed, adrenal androgens have been shown to influence brain function in laboratory animals, and are included in the family of neuroactive steroids (Spear 2000). There is preliminary evidence that DHEAS levels may be linked to aggression in middle childhood, and high levels of DHEAS have been found in samples of children (mostly boys) diagnosed with Conduct Disorder (CD) and Oppositional Defiant Disorder (ODD; van Goozen et al. 1998; 2000). In female rodents and primates, DHEA reduces aggression, although it is still unknown whether this also applies to humans (Simon & Lu 2006). Hyperactivity symptoms in a sample of children with Attention Deficit Hyperactivity Disorder (ADHD) correlated with lower DHEA and DHEAS levels in a study by Strous et al. (2001). Finally, it has been proposed (Herdt & McClintock 2000; McClintock & Herdt 1996) that adrenarche could be responsible for the onset of the first sexual/romantic attractions, usually happening at about 7–10 years of age. Thus, adrenal androgens appear to be involved in sexual differentiation and in the initiation of early reproduction-related behavior in middle childhood.

When adrenal androgens start to be secreted, and locally converted to active molecules, previously unexpressed genetic variation in the sex-hormones pathways will suddenly be uncovered and rendered effective. Such variation may include allelic variants in the many enzymes involved in hormone production, conversion, transport, reception, and degradation, all of which can potentially affect behavior. For example, sequence variants in the androgen receptor (*AR*) gene have been linked to life-history variables such as aggression, impulsivity, number of sexual partners, age of menarche, and likelihood of having divorced parents (Comings et al. 2002; however, the results were not replicated in a large study by Jorm et al. 2004). In addition, the activation of sex-hormone pathways is bound to interact with the organizational effects of prenatal and perinatal hormone levels. The rising levels of sex hormones in the brain, coupled with the release of sex-hormone related genetic variation, would determine a "modular" phenotypic transition between childhood and juvenility, where both sex-specific and heritable factors would come into play. This is consistent with the evidence of a relatively rapid, sex-specific reorganization of attachment patterns at about 7 years of age. But what is the relationship between sex hormones and attachment?

7.2.2. Sex hormones, stress, and attachment behavior: A complex interplay. Life-history models are usually centered on the effects of stress and attachment on sexual development: psychosocial stress and insecure attachment are expected to (1) accelerate sexual maturation (adrenarche in both sexes, and puberty in girls) and (2) affect a suite of reproduction-related behaviors (e.g., aggression, impulsivity), many of which are under the influence of sex hormones. The hypothesis I propose focuses precisely on the reverse effect, that of sexual development on attachment and, by definition, on stress regulation. Experimental evidence from nonhuman animals strongly suggests that sex hormones can directly affect attachment-related behaviors: testosterone administration dramatically reduces separation-induced distress vocalizations in chicks, quails, and guinea pigs (Bernroider et al. 1996; Panksepp 1998), whereas prenatal administration of estrogens seems to exert the opposite effect. In rhesus monkeys, too, prenatal testosterone has been found to influence the sex-specific development of separation vocalizations (Tomaszycki et al. Wallen 2001; Wallen 2005).

In a broader perspective, there is ample evidence that sex hormones deeply interact with stress-regulation mechanisms. Taylor et al. (2000) summarized a wide array of studies and argued that, in many animals (including humans), the stress response system of adults shows adaptive sexual dimorphism. The classic fight-or-flight response seems to be more characteristic of males, whereas the primary response of females is better described as "tend-and-befriend." In other words, stress tends to induce aggression and/or avoidance in males, but it solicits caregiving (protection of offspring) and seeking of social support and affiliation in females. The prevalence of the tend-and-befriend response is thought to depend on the kind and level of experienced stressors, and on the female's reproductive status (e.g., on whether she is sexually mature, has dependent offspring, and is in a fertile phase). At the neurobiological level, this sexual dimorphism could be mediated by oxytocin and endogenous opioids, and would therefore be closely linked to the neural substrate of the attachment system (Keverne et al. 1999; Taylor 2006; Taylor et al. 2000). Sex hormones have a critical role in this pathway: androgens, for example, inhibit the stress-induced release of oxytocin, while estrogen enhances the anxiolytic effects of oxytocin (see Jezova et al. 1996; McCarthy 1995; McCarthy et al. 1996). Sex hormones can also directly affect the stress system through regulation of neuroendocrine activity in the amygdala (Viau 2002). Other mechanisms of interplay among sex hormones, stress, and aggression have been described in an evolutionary perspective by Korte et al. (2005).

It is noteworthy that the fight-or-flight versus tend-and-befriend model closely mirrors the sex differences observed in avoidant versus anxious attachment styles; in particular, anxious strategies involve heightened seeking of support and closeness, which is typical of the female response to stress. From the above discussion, it is apparent that the stress/attachment system and the sexual system can interact bidirectionally across the life cycle; for example, psychosocial stress leads to accelerated adrenarche, which, in turn, could affect the stress-regulatory pathways (already primed by early experience) with both sex-specific and genotype-dependent effects. Such positive feedback mechanism could then function as effective developmental "switches," leading to diverging life history trajectories. Many interesting questions arise from this hypothesis. Could attachment behaviors be related to prenatal sex hormone levels (which organize early brain development)? Might the relationship become manifest only starting from middle childhood, because of the activational effects of adrenal androgens? Are sex hormones the vehicle of genetic effects on the K-factor, with its overlap with attachment and mating styles? And are atypical degrees of masculinity/femininity related to "sex-atypical" attachment patterns, for example, in highly anxious men? A preliminary study (cited in Greenberg 1999) found an association between ambivalent attachment and gender identity disorders in childhood, but the evidence regarding this issue is still very limited.

In summary, powerful hormonal changes take place at the start of middle childhood, and we are only beginning to understand their full implications for human development. The "hidden" onset of pubertal maturation brought about by adrenarche might be the neuroendocrine switch that begins to reorganize attachment towards its mating-related functions, even before the coming of full reproductive maturity. While this hypothesis is still speculative, it provides a starting point to investigate the relationships among attachment, reproduction, and the hormonal mechanisms that regulate life history strategies (Adkins-Regan 2005; Ellison 2001).

8. Conclusion

The study of reproductive strategies has become a fruitful, fast-expanding area of research in evolutionary psychology and anthropology. More broadly, life-history theory is emerging as a truly integrative paradigm in the study of individual differences, encompassing traditionally separated fields of inquiry such as attachment theory, the psychology of aggression and sexuality, personality theory, behavior genetics, and the anthropology of mating systems. The next frontier will be achieving integration with psychobiology and neuroscience, and this enterprise is already underway; see, for example, the evolutionary model of stress reactivity by Boyce and Ellis (2005; Ellis et al. 2006), and the work by Korte et al. (2005) on alternative phenotypes in stress regulation and aggression. I anticipate that, in this integration process, the study of sex differences and sexual selection will play an increasingly central role. Males and females face different strategic choices, and different evolutionary pressures, at each stage of their life cycle. Understanding how male and female strategies unfold (and interact) in the course of development is an essential step for appreciating the fascinating complexity and the deep evolved logic of human life histories.

ACKNOWLEDGMENTS

I am deeply grateful to Jay Belsky and Alasdair Houston for their precious comments, and for the creative and rewarding discussions we had on attachment theory and evolutionary biology. I also owe much to Jim Chisholm, Sarah Hrdy, Susan Johnson, Bruce Ellis, and an anonymous reviewer for their help in sharpening the theory, catching mistakes, and (not least) writing a much clearer paper. Kathryn Kerns and Ildiko Toth kindly shared their original data for reanalysis. Finally, Marinus van IJzendoorn, Marion Bakermans-Kranenburg, Mattie Tops, Fabiënne Naber, Cristina Becchio, Angela Ciaramidaro, Livia Colle, Elisa Grandi, Valeria Manera, and Davide Mate all provided useful feedback on previous versions of the manuscript.

NOTES

1. The distinction I draw here between past-focused interviews and present-focused questionnaires is a simplification: there are also interviews about current relationships and questionnaires about past attachment experiences. However, they are employed much less often than the "paradigmatic" instruments I discuss here, so my distinction holds as a general approximation.

2. When adaptive variations in life history parameters are condition-dependent, rather than genetically determined, some authors suggest they should be labeled life history *tactics*, since they can be seen as conditional branches of a single state-dependent strategy (e.g. Gross 1996). However, since the term "strategy" has gained common use and other authors use "tactic" with different meanings, I refer to reproductive strategies throughout this article.

3. This kind of mechanism might explain the finding by Quinlan (2007) that, with increasing pathogen stress, paternal involvement decreases linearly while maternal care follows a quadratic function (first increasing, then decreasing). The increase in maternal care at moderate levels of risk could reflect mothers "compensating" for lowered paternal investment.

4. The letter "K" in the K-factor derives from the classic approach to life history theory, based on population growth rates. In this theoretical framework, slow and high-investment strategies are labeled "K-strategies," while fast and low-investment strategies are labeled "*r*-strategies." While this approach was popular some decades ago, most life-history theorists presently favor models based on age-specific mortality patterns and extrinsic risk (see sect. 5).

5. As discussed in section 2.3, stability in attachment security is not always expected to be high; in particular, negative life events often lead to shifts towards insecurity, which have the effect of decreasing measured stability. The "prototype" model discussed by Fraley (2002), however, implies that early security exerts continuing effects during development, both in low-risk and high-risk environments.

Open Peer Commentary

Selfishness and sex or cooperation and family values?

doi:10.1017/S0140525X09000028

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Abstract: Evolutionary models of behavior often encounter resistance due to an apparent focus on themes of sex, selfishness, and gender differences. The target article might seem ripe for such criticism. However, life history theory suggests that these themes, and their counterparts, including cooperation, generosity, and gender similarities, represent two sides of the same coin – all are consequences of reproductive trade-offs made throughout development.

Evolutionary approaches to human behavior, such as Del Giudice's target article, have been accused of overemphasizing: (1) a limited (and often unsavory) set of topics, especially sex and mating; (2) selfishness; and (3) gender differences (see also Kenrick et al. 2003). Each of these accusations is superficially true but is misguided at a deeper level. The approach presented in the target article helps emphasize this latter point.

1. Sex. An evolutionary approach is fundamentally concerned with reproduction, but reproduction involves more than just sex. Life history theory presumes that all organisms are designed to allocate resources over the lifespan in a way that maximizes reproductive success. Mating effort is certainly a central phase of any organism's life history. For salmon and century plants, which reproduce in a single burst and then die, the effort ends there. But for many organisms, including all mammals, the effort expended in attracting a mate and copulating is relatively minor compared to the effort devoted to parenting. In the case of humans, decades of parenting effort may precede decades of grandparental effort. From this perspective, reproductive strategy incorporates not only parent–child and parent–parent bonding, but also many other non-obvious aspects of life, including religious attendance and political affiliation (e.g., Weeden et al. 2008). As suggested by Del Giudice, interpersonal attachment patterns may also reflect general reproductive strategies, and trade-offs between mating and parenting effort.

2. Selfishness. Selfish genes do not necessarily produce selfish organisms. Although genes tend to promote their own relative replication rates (Dawkins 2006; Williams 1966), those genes often construct organisms that make trade-offs favoring cooperation and kindness over narrow selfish behaviors. At the simplest level, people are often kind and generous to kin and to those with whom they expect to have future interaction (e.g., Ackerman et al. 2007; Burnstein et al. 1994). Economists and game theorists have been surprised at people's willingness to cooperate with others even when payoffs favor competition, but given the diffusion of genetic returns generated by common human social arrangements, people's generosity seems less irrational (Kenrick et al. 2008). For instance, a view of organisms as selfish might suggest that in a domain such as romantic relationship formation, which is so closely linked to genetic payoffs, competitiveness will rule the day. Yet, people cooperate in order to improve a range of reproductive goals (e.g., Ackerman & Kenrick, under review). Perhaps even more economically puzzling is the fact that people regularly turn down offers of resources from others, even when they are actually in need of help. Viewed within the framework of life history theory, such self-denial is often self-serving at a more ultimate level (Ackerman & Kenrick 2008). Indeed, "irrational" behaviors, such as cooperative courtship and refusing offered aid, may be consequences of the very same trade-offs that produce secure and insecure attachment patterns.

3. Gender differences. Gender differences reflect critically important trade-offs, but so do gender similarities. Life history theorists have noted that reproductive strategies often diverge within a species, many times along gender lines. The underlying cause of such variation – differences in minimal obligatory parental investment – can result in a wide range of sex differences, from mate preferences (for willingness to engage in short-term relationships; Li & Kenrick 2006) to benevolence (between friends; Ackerman et al. 2007) to attachment patterns (in insecure attachment; Del Giudice, target article). For instance, in research on cooperative courtship, we find evidence that parental investment differences may motivate women to prefer assistance in building thresholds for potential mates, but motivate men to prefer assistance in overcoming these thresholds (Ackerman & Kenrick, under review). At the same time, gender similarities reveal equally important trade-offs. In biparental species (e.g., humans), many of the problems of parenting and mating are the same for males and females, and solutions to these problems play out through sex similarities in some of the same arenas that also exhibit sex differences – mate preferences (for partner qualities within short-term relationships; Li & Kenrick 2006), benevolence (between kin; Ackerman et al. 2007), and attachment patterns (in secure attachment; Del Giudice, target article). Indeed, in our studies of cooperative courtship, we find substantial similarities between men's and women's desires to cooperate, despite sex differences in how this cooperation materializes (Ackerman & Kenrick, under review).

4. Conclusion. Life history theory is garnering increased attention among behavioral researchers. At first blush, the evolutionary foundations of this theory might inspire familiar objections. On careful consideration, however, a theoretical and empirical response to these objections reveals even broader application for an evolutionary life history perspective. This approach suggests that variations in a wide range of phenomena (e.g., attachment patterns, cooperation and competition, selfishness and generosity) emerge from a common source: trade-offs concerning reproduction (but not just sex!). As Del Giudice's target article implies, the next stage of inquiry involves a full conceptual integration of these important ideas with the range of phenomena in the behavioral sciences.

No reliable gender differences in attachment across the lifespan

doi:10.1017/S0140525X0900003X

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Abstract: In middle childhood, boys show more avoidant attachments and girls more ambivalent attachments as a prelude to gender differentiation in reproductive strategies. However, we have failed to find systematic and method-independent gender differences in middle or late childhood attachments, nor in adult attachment representations. We conclude that Del Giudice's model rests on a brittle empirical basis.

Del Giudice's model of different reproductive strategies for females versus males hinges critically on the assumption that boys show more avoidant attachments and girls more ambivalence in the developmental period after early childhood. Attachment research in infancy and early childhood did not detect gender differences, whereas, according to Del Giudice in the target article, the picture changes "dramatically" in middle childhood. The question we address here is: Does the picture indeed change, and if so, in what respect?

Del Giudice lists seven studies to document this radical change. The three studies using the Coping Strategies Questionnaire (CSQ) should, however, be discounted as sources of evidence because patterns of attachment behavior and mental representations of attachment cannot be validly assessed by means of self-reports. Children as well as parents lack insight into their own attachment interactions and relationships, in particular when they are insecurely attached. Their insecurity distorts their self-perception (for meta-analytical evidence, see Van IJzendoorn et al. 2004).

Four pertinent studies remain (Del Giudice, in press; Granot & Mayseless 2001; Kerns et al. 2007; Toth et al., personal communication, October 19, 2007). Only the Kerns et al. (2007) study produced results contrasting with Del Giudice's model, showing that female 9–11-year-olds were more often classified as avoidantly attached relative to male participants. The other studies pointed to the expected direction of insecure boys being more often avoidant and insecure girls more often ambivalent.

In our Leiden Attachment Research Program, we assessed quality of attachment in two studies on 7-year-old children (Gilissen et al. 2008; Pannebakker 2007), and in one study on 14-year-olds (Beijersbergen et al., in press). Furthermore, after a brief literature search, we found pertinent studies by Ammaniti et al. (2000), Bureau et al. (2006), and Gloger-Tippelt and Koenig (2007) on children aged 6–10 years. Following on Del Giudice's focus on the secure, avoidant, and ambivalent categories, we excluded the category of disorganized attachment, or used forced classifications when available. The combined distribution of secure, avoidant, and ambivalent attachments across all samples (including those discussed by Del Giudice) is 49% secure, 37% avoidant, and 14% ambivalent attachments for boys. For girls, the distribution is 64% secure, 22% avoidant, and 14% ambivalent attachments (see Table 1). Haberman's adjusted standardized residuals show significant differences between boys and girls for the secure (fewer boys) and the avoidant (more boys) classifications, but not for the ambivalent classification.

Dividing the studies according to their assessment procedures (doll play narratives based on Bretherton et al. 1990; Cassidy 1988), observations of separation/reunion (Main & Cassidy 1988), and modified Adult Attachment Interview (AAI; Hesse 1999; Main et al. 1985), we only found gender differences in the set of studies using narratives (see Table 1). Apparently, the gender effect is measurement-specific, and systematic errors of measurement

Table 1 (Bakermans-Kranenburg & Van IJzendoorn). *Distributions of attachment in middle childhood and adulthood*

	Secure (n; %)	Avoidant (n; %)	Ambivalent (n; %)	Total (N)	Secure	Avoidant	Ambivalent residuals*
Total, 6–14 years	n %	n %	n %	N	Haberman's adjusted standardized residuals*		
Boys	179; 49%	134; 37%	53; 14%	366	***− 4.6***	***4.8***	*0.4*
Girls	342; 64%	117; 22%	72; 14%	531	***4.6***	***− 4.8***	− 0.4
Doll play narratives[1]							
Boys	123; 51%	88; 36%	31; 13%	242	***− 3.9***	***4.4***	− 0.1
Girls	210; 67%	61; 20%	41; 20%	312	***3.9***	***− 4.4***	*0.1*
Observation (separation-reunion)[2]							
Boys	27; 69%	7; 18%	5; 13%	39	*0.2*	***− 0.2***	*0.4*
Girls	84; 69%	24; 20%	13; 11%	121	***− 0.2***	*0.2*	− 0.4
AAI (modified for younger ages)[3]							
Boys	29; 34%	39; 46%	17; 20%	85	***− 2.0***	*1.8*	*0.3*
Girls	48; 49%	32; 33%	18; 18%	98	***2.0***	***− 1.8***	− 0.3
AAI [4]							
Males	331; 48%	230; 33%	126; 18%	687	***− 1.0***	*1.8*	− 0.8
Females	1507; 50%	901; 30%	589; 20%	2997	*1.0*	***− 1.8***	*0.8*

*Significant adjusted standard residuals in bold

[1] Del Giudice (2008); Gilissen et al. (2008); Gloger-Tippelt et al. (2007); Granot & Mayseless (2001); Kerns et al. (2007); Toth et al. (2006)

[2] Bureau et al. (2006); Pannebakker (2007)

[3] Beijersbergen et al. (in press); Ammaniti et al. (2000)

[4] Van IJzendoorn & Bakermans-Kranenburg (in preparation)

might be the source of these differences. Narrative procedures might focus more on content than on coherence, contaminating formal avoidance with substantive "macho" accounts. In addition, differences in verbal abilities between boys and girls in this age group may play a role (Verschueren & Marcoen 1999). It should be noted that in Granot and Mayseless' (2001) study, secure children (mostly girls) had significantly higher scores on cognitive achievement, and avoidant children (predominantly boys) had the lowest scores on cognition.

Furthermore, the gender difference in studies with doll play narratives is restricted to boys showing more avoidant attachments, and not less or more ambivalence than girls. In the narrative approach, boys do follow the predicted pathway of avoidance, but girls do not prefer the ambivalent attachment strategy (see Table 1). In the observational studies, no gender differences in middle childhood have been documented. In the two studies using the AAI, boys were only slightly under-represented in the secure category and were not significantly over-represented in one of the insecure categories (Table 1).

It should be noted that numerous studies on attachment representations in adulthood using the Adult Attachment Interview – the gold standard for assessing attachment representations, which is independent of cognitive abilities (Hesse 1999) – have not come up with any replicable gender differences in dismissing versus preoccupied attachments. In a meta-analysis of studies using the AAI (Van IJzendoorn & Bakermans-Kranenburg 1996), and in a recent update (Van IJzendoorn & Bakermans-Kranenburg 2008; in preparation), we traced 17 studies on 687 males and 59 studies on 2997 females (mostly parents of reproductive age). The distribution of males was 33% dismissing, 48% secure, and 18% preoccupied attachments, while the distribution of females was 30% dismissing, 50% secure, and 20% preoccupied attachments. No significant gender difference was found (see Table 1).

We conclude that Del Giudice's model has a brittle empirical basis. We did not find systematic and method-independent gender differences in middle- or late-childhood attachments, nor were any gender differences in adulthood present in studies using the gold standard to assess attachment representations. The speculative model badly needs some repairs to accommodate with an obstinate empirical reality.

Attachment, reproduction, and life history trade-offs: A broader view of human mating

doi:10.1017/S0140525X09000041

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Abstract: In this commentary, we attempt to broaden thinking and dialogue about how our ancestral past might have affected attachment and reproductive strategies. We highlight the theoretical benefits of formulating specific predictions of how different sources of stress might impact attachment and reproductive strategies differently, and we integrate some of these ideas with another recent evolutionary model of human mating.

According to Del Giudice's model, sex differences in insecure attachment orientations should emerge most strongly when individuals are exposed to moderate levels of stress during development. In such environments, males should be more likely to develop avoidant attachment orientations, and females ought to develop anxious/preoccupied orientations, especially from middle childhood extending into early adulthood. There are two potential problems with this claim. First, valid attachment measures have proven difficult to develop for middle childhood (Kerns 2008), which may partially explain the dearth of studies focusing on this age group. Second, gender differences are rarely found or are quite small in adult samples, regardless of whether self-report or interview measures of attachment are used (Crowell et al. 1999/2008). It is not clear how Del Giudice's model reconciles these issues.

When contemplating how stress impacted social development in the environment of evolutionary adaptedness (EEA), one must consider the different sources of stress our ancestors faced and which specific sources were most strongly associated with certain environmental risks, given humans' comparatively long life histories. According to life history theory (Kaplan & Gangestad 2005), organisms make trade-offs between current versus future reproduction, quality versus quantity of offspring, parental investment versus offspring genetic quality, and reproduction versus survival over the lifetime. Different sources of stress might have had unique implications for certain life history trade-offs and, ultimately, the adoption of certain adult reproductive strategies.

Four prevalent environmental threats during evolutionary history were predation pressures, the availability of food, the prevalence of diseases, and intergroup or intragroup conflict (Simpson & Belsky 2008). Each type of threat could have produced a unique source of stress that affected how life history trade-offs were made. For example, if diseases were prevalent in the local environment, most men might have placed more weight on either offspring quantity or their genetic quality, contingent on other mating factors. Most women, however, should have emphasized offspring genetic quality on account of the more limited lifetime reproductive capacity of women and the need to bear the most disease-resistant offspring. These trade-offs may have oriented both sexes toward greater avoidance, which might have facilitated greater male promiscuity and more male–male intrasexual competition (Schmitt 2005b). Women should have been more strongly attracted to mates who displayed better health or more viability, and women should have competed more intensely to reproduce with these men, putting less emphasis on paternal investment.

In environments characterized by intergroup conflict, many men may have shifted to a shorter-term, higher-quantity mating strategy, given the greater risk of death in ancestral men (Cronin 1991). Most women, however, may have worked to keep their mates invested to secure more protection for themselves and their offspring. Adopting an avoidant orientation might have been the best way for most men to increase their fitness in these environments, whereas an anxious/preoccupied orientation might have been the best strategy for most women. The main point is that different sources of stress might have shifted men and women in the same or in different directions with respect to adult attachment orientations and reproductive strategies, even if the absolute levels of stress experienced during development were similar.

Although the purpose of the target article is to present an integrated life-history-based evolutionary model of reproductive strategies, relatively little is said about how life history trade-offs might intersect with proximal (current) trade-offs. In section 6.3.1 of the target article, the author notes that "women cannot shift the balance between parenting and mating effort as easily as men." This is precisely why ecologically contingent evolutionary models of human mating such as the Strategic Pluralism Model (SPM; Gangestad & Simpson 2000) have been developed.

Rather than viewing human mating in terms of how an individual's history results in specific adult reproductive strategies, SPM proposes that women evolved to make mating decisions on the basis of the nature of their current local environments. Specifically, women should place relatively greater weight on men's viability (i.e., their health, vigor, and ability to withstand diseases), especially in pathogen-prevalent environments. However, they should place greater emphasis on men's ability and willingness to invest in themselves and their offspring when local environments require more biparental care. Indeed, it is precisely because women cannot easily "shift the balance" between parenting and mating effort that they should have evolved to select mates by making judicious trade-offs between these mate attributes. SPM, therefore, explains how and why women evolved to make the best of one "constraint" imposed on them by nature – the unique way in which they reproduce. A complete evolutionary account of human mating must consider how and why both ontogenetic (life history) and proximal (current environmental) factors led both sexes to make adaptive decisions with respect to the allocation of mating effort versus parenting effort.

How might life-history and ecological-contingency models intersect? An individual's developmental history could set thresholds for judging the acceptability of a mate's viability or investment potential in adulthood. For example, females exposed to early life stress stemming from prevalent diseases should have placed greater value on – and may have had higher thresholds of acceptability for – a mate's degree of viability. Conversely, women should have placed more weight on the willingness and ability of mates to invest if the primary source of early stress was poor or unpredictable food supplies. The important point is that the specific source of psychosocial stress in a person's past could influence her or his tendency to value, attend to, and hold higher or lower standards of acceptability for a potential mate's viability in relation to investment potential, or vice versa. These standards may also have influenced decisions about whether and when to terminate relationships.

Though taken for granted in modern environments, our ancestors faced major obstacles in raising even a few offspring to adult reproductive age. Selection pressures should have led people to generally make adaptive trade-offs on the basis of reproductively relevant events that occurred earlier in their lives. However, selection pressures should also have led people to make adaptive trade-offs in response to reproductively relevant conditions in their current environments. Long-term fitness returns might actually have been more strongly linked to the mating and parenting trade-offs that individuals made in response to their current environments in adulthood than to more distant life-history factors, especially if factors that affected mating or parenting changed within a person's lifetime (e.g., the prevalence of disease, sex-ratios, changes in the food supply).

"Fatal attraction" syndrome: Not a good way to keep your man

doi:10.1017/S0140525X09000053

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Abstract: Female behavior that is driven by ambivalent attachment is far from passive or withdrawn. As dramatised in the movie "Fatal Attraction," such women's emotional hyper-reactivity is often expressed in violence, which is antithetical to securing investment from mates or peers. Single motherhood, rather than reflecting an avoidant strategy in which close relationships are devalued, is often the result of ecological conditions in which paternal investment is desired but unavailable.

Does the "fearfulness, withdrawal, and passive behavior" that Del Giudice notes (target article, sect. 6.3.2, para. 2) is associated with an ambivalent attachment style, really assist women in retaining their partner and in maximising paternal investment? Preoccupied attachment is characterised by intense desire for closeness, discomfort when not intimately involved with another, and nagging worry about rejection. It is a short step from here to the clinical condition of borderline personality disorder (BPD), with its pervasive relationship instability and frantic efforts to avoid separation or abandonment.

Initial idealisation of the target is coupled with demands for their exclusive attention, but at the first sign of real or imagined rejection, the emotion switches from infatuation to bitter devaluation.

Dependent and borderline personality traits characterise up to 50% of male perpetrators of partner violence, with these men's extreme dependency resulting in a violent response to the wife's perceived rejection or insubordination (Holtzworth-Munroe & Stuart 1994). Following the belated recognition of symmetry in partner violence, women's partner violence has also been related to attachment style. Women receiving mandated treatment for domestic violence show elevated rates of both anxious and avoidant attachment styles and evidence of borderline personality traits (Goldenson et al. 2007). Perhaps because 75% of BPD sufferers are women, there has been a tendency to consider it as a predominantly internalising disorder by emphasising the diagnostic criteria of chronic feelings of emptiness, suicidal behaviour, and self-mutilation.But there are other externalizing diagnostic criteria, including affective instability, impulsivity, and "inappropriate, intense anger or difficulty controlling anger (e.g., frequent displays of temper, constant anger, recurrent physical fights)" (American Psychiatric Association 2000, p. 710).

Self-harm is more strongly associated with an avoidant attachment style, while it is anxious attachment that is associated with reactive, other-directed intimate aggression (Critchfield et al. 2008). College women with attachment styles characterised by high anxiety and low avoidance are more likely to report having used violence than women who are high in both styles (Orcutt et al. 2005). These violent reactive outbursts, characteristic of BPD, have been linked to hyper-responsiveness of the amygdala and modulatory failure of the prefrontal cortex (Siever 2008). In short, although Del Giudice suggests that "anxious behaviors (e.g., dependence, preoccupation with intimacy and partner availability) can help to maintain closeness with one's partner" (sect. 6.3.1, para. 4), there is evidence that insecurity of this kind can have exactly the opposite effect.

With regard to same-sex relationships, I agree with Del Giudice that the adaptive benefits of an anxious attachment style for women are unclear. That anxious traits are "not nearly as damaging for females as they are for males" (sect. 6.3.2, para. 2) is hardly a ringing endorsement of their functionality. Female friendships are characterised in the psychological literature as more exclusive, self-disclosing, supportive, and lacking the competitive edge of male groups (see Rose & Rudolph 2006). However, this rosy view belies a more complex picture. A preoccupation with friendships and emotional intimacy fuels girls' need for social approval, increases possessive feelings and jealousy about best friends, and results in depression when friendships terminate (which they do with greater frequency among girls than among male friends). If these are the downsides of "normal" girls' friendships, they are surely multiplied for anxiously attached girls.

Low self-worth is associated with heightened "best friend" jealousy, loneliness, social rejection, and aggression (Parker et al. 2005). Conflict between teenage girls is often driven by rivalry about attractiveness to the opposite sex and "ownership" of desirable boys (Campbell 1995). If anxious girls accord high strategic priority to securing male investment, this should increase their willingness to compete for it, drawing them into indirect or direct aggression against their peers.

Before considering a female's avoidant strategy, I need to pose a more wide-ranging question about life history strategies. What is their psychological status? Attachment security might shape later reproductive strategy in several ways. Early experience might affect personality traits, molding an individual's general level of anxiety or avoidance in response to others. These traits would alter interpersonal competence (the ability to form stable relationships). If early experiences build a "behavioral-motivational" system, they might act through preference, by causing the individual to value some relationship styles more than others, as exemplified by Del Giudice's statement "preoccupied individuals eagerly look for intimate relationships" (sect. 5.2, para. 4). More cognitively, early experiences may lead to different "decisions concerning reproductive strategy." The implication here is that individuals weigh the costs and benefits of different strategies (with those weightings informed by early experience) to arrive at some personal utility function. In short, is the link between early experience and later strategy mediated by personality (avoidant women are unable to cope with long-term relationships), preference (avoidant women prefer short-term sexual encounters), or cognition (avoidant women decide that the net utility of pair-bonding is lower than that of single motherhood)?

Psychologically damaged individuals are certainly poor at maintaining stable relationships, but this is not equivalent to preferring short-term relationships or devaluing stable relationships. Among girl gang members, most of whom came from very disturbed families, I was surprised by the extent to which they idealised marriage and traditional family values (Campbell 1992). Their chaotic and marginal lifestyles, coupled with volatile emotions, often conspired to defeat long-term relationships; but there was little doubt that the girls very much aspired to them (LeBlanc 2004). As for an active preference for short-term encounters, recent data suggest that women find one-night stands very much less emotionally satisfying than do men (Campbell 2008b). Young single mothers rarely choose their situation: Local female-biased sex ratios (resulting from male death, imprisonment, and addiction) create a paucity of men who are able or willing to make paternal investment (Campbell 1995). "Avoidance" may be less of a female strategy than a default option forced by ecological circumstance.

Avoidant strategy in insecure females

doi:10.1017/S0140525X09000065

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Abstract: This commentary cites evidence to argue that girls growing up in a competitive and aggressive environment are more likely to shift to avoidant attachment than to ambivalent attachment in middle childhood. These avoidant women are also more likely to favor a short-term mating strategy. The role of oxytocin (OT) and early experience in shaping an avoidant attachment in females is also discussed.

Del Giudice's evolutionary model integrating attachment with human reproductive strategies contributes to our understanding of the adaptive significance of gender differences in attachment, and of the role of sex-related endocrine mechanisms on development of attachment styles. He argues that gender differences in attachment patterns emerge during middle childhood, and specifically, that insecure girls tend to develop ambivalent attachment, whereas insecure boys develop avoidant attachment, when faced with new social demands driven by the peer group.

If this argument is correct, we should expect that insecure girls, similar to boys, would be more likely to shift to avoidant attachment in middle childhood. Thus, this commentary cites evidence supporting why this shift to avoidant attachment is essential. We follow Del Giudice's logic in analyzing the emergence of aggression as a correlate of avoidant attachment in girls at this stage of childhood.

According to Del Giudice's analysis of attachment styles in middle childhood, insecure children without a secure family environment must "begin to fight their way through social reality" (target article, sect. 7.1.2). Therefore, insecure girls are more likely to shift to avoidant styles than ambivalent styles,[1] which emerge from competition in the peer group. The behavioral correlates of avoidant attachment (i.e., aggression) are already selected at this stage because they are more adaptive than traits associated with ambivalent attachment (e.g., dependency, behavioral immaturity, and passivity in peer relations) in terms of independent resource acquisition because insecure girls cannot rely on their parents under extreme high-risk environmental conditions.

Guttmann-Steinmetz and Crowell (2006) provide a conceptual model demonstrating that externalizing behavior by children develops from parental failure to provide a secure base to protect children from environmental risks. With the recent development of measures of attachment quality during middle childhood (Finnegan et al. 1996; Kerns et al. 2000), a line of research has emerged suggesting that girls' aggression is associated with avoidant rather than ambivalent attachment style. No gender differences were found in the association between avoidant attachment and aggression (Davies & Forman 2002; Granot & Mayseless 2001). Finnegan et al.'s (1996) research showed that for both sexes, aggression was predicted by an avoidant strategy but not by a preoccupied strategy, according to their specific linkage hypothesis. More recent research (Booth-LaForce et al. 2006) showed that avoidant coping in relation to the mother, and lower security with the father, was related to aggression. These associations did not vary by sex of child. In addition, in order to reduce the risk of retaliation, girls are more likely to use subtle forms of aggression such as relational aggression or coercive and prosocial strategies of resource control (i.e., bi-strategy; Hawley 2007) to compete for resources, such as better-resourced men (Campbell 1999). Active reaction (the correlates of avoidant attachment) to secure a scarce resource is likely to be more effective than a passive one (the correlates of ambivalent attachment).

We would expect insecure females to be more likely to adopt avoidant rather than anxious strategies to maximize current reproductive success, no matter how challenging the environment is,[2] because there is very limited support for the proposal that an anxious strategy enhances partner investment or reproductive success. However, "avoidant" women who show little desire for commitment and adopt a short-term mating strategy (Feeney 1999; Gentzler & Kerns 2004) by mating with multiple males could acquire considerable resources and simultaneously reduce the possibility of future male attacks against her and her offspring (Hrdy 1981).

In accordance with Del Giudice's hormonal basis of the middle childhood transition, we now consider the evidence for the role of oxytocin (OT) in females' avoidant attachment. OT is closely implicated in female behavior because its effects are strongly modulated by estrogen. Early social experience can alter social behavior by affecting the development of neuroendocrine systems including OT (see Cushing & Kramer 2005, for a review). In rats, female offspring raised by high-licking and high-grooming mothers show a significant increase in oxytocin receptors, OTRs (Francis Young et al. 2002). Furthermore, changes in the oxytocinergic system in response to social interaction could alter brain development and, thereby, the subsequent expression of social behavior. However, OT has little or no effect on regions of the brain in adults due to a lack of receptors, compared with before adolescence (Cushing & Kramer 2005). Thus, middle childhood appears to be the "last chance" for OT to exert long-lasting effects on behavior. In a high-risk environment lacking sufficient parental investment, we would expect to see a decrease in oxytocin affecting the childhood organization and development of the brain and resulting in an increase in aggression among girls with insecure attachments. In an environment in which well-resourced males are in short supply, it would seem adaptive that female competition and female assault (see Campbell 1999) would be primed by epigenetic mechanisms of early social experience (Cushing & Kramer 2005).

Overall, we welcome and accept most of Del Giudice's arguments as a significant contribution to our understanding of the development of attachment from an evolutionary perspective. However, Del Giudice's analysis of insecure attachment in females should include avoidant pattern, which should be further examined empirically.

ACKNOWLEDGMENTS

We thank Anne Campbell and Lei Chang for comments on this manuscript.

NOTES

1. Del Giudice admits that it is not clear whether ambivalent pattern is adaptive to girls (see target article, sect. 7.1.2).

2. According to Del Giudice's argument, there is no opportunity for insecure girls to shift to a secure attachment even in a secure environment because insecure attachment patterns after the middle childhood transition are expected to be stable in adulthood.

Attachment and life history strategy

doi:10.1017/S0140525X09000077

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Abstract: Del Giudice addresses a complex and pertinent theoretical issue: the evolutionary adaptiveness of sex differences in attachment styles in relation to life history strategy. Although we applaud Del Giudice for calling attention to the problem, we regret that he does not sufficiently specify how attachment styles serve as an integral part of a coordinate life history strategy for either sex.

Del Giudice's target article addresses a complex and pertinent theoretical issue: the evolutionary adaptiveness of sex differences in attachment styles as they relate to life-history strategy. This is an extremely important theoretical problem in evolutionary psychology, and we applaud Del Giudice for bringing it to the attention of the field; but we are not convinced that the present article makes a very substantial contribution to its resolution. Although the theory seems plausible, Del Giudice does not make the necessary theoretical connections to sufficiently integrate these two constructs.

One major limitation is that Del Giudice mentions certain important issues that are critically relevant to the topic, but rather than explaining them or taking a position on them, he claims that they are beyond the scope of the article. For example, he does not address whether or not attachment patterns are categorical or continuous, and instead references the work of Fraley and Spiker. Del Giudice must take a stand on this issue if he is going to take an evolutionary stance on attachment patterns based on individual differences – in our understanding, specifically in the direction of the patterns being continuous. He also does not fully address the degree of persistence versus plasticity of "internal working models" across the life cycle, stating that "a detailed treatment of the issue is beyond the scope of this article" (sect. 2.3, para. 1). Without explaining these issues in more detail, the conclusions seem based more on belief than on a principled deliberation on the evidence.

Aside from the lack of explanation, Del Giudice also makes contradictory statements without offering a resolution. For example, Del Giudice discusses the affect of increasing age on life history trade-offs, with aging men switching from mating effort to parental investment. He argues that "this transition may be especially dramatic in insecurely attached men" (sect. 7.1.3, para. 3). However, prior to this he discusses a couple of studies finding that "short-term mating in men tended to increase with age, and men were on average more oriented with short-term mating regardless of attachment style" (sect. 6.4.1, para. 2). This is an apparent contradiction that is left unresolved.

Del Giudice also discusses "disorganized" attachment style early in the article, stating later that it will not be integrated into his synthesis on account of three concerns about the concept. However, in the very next paragraph he mentions it again, arguing that it is the only infant attachment pattern showing a sex difference. If one of the main points of this article is to discuss theoretical reasons for sex differences in attachment, this issue may be of critical importance. Granted, Del Giudice suggests that this is an important area of research for the future, but because he has written this *BBS* target article specifically on the topic of evolutionary perspectives on sex differences, he needs to offer his perspective on why that one notable infant sex difference may exist.

One might argue, for example, that an infant's attachment style has a different function than an attachment style displayed during adolescence or young adulthood. At each point in time, the goals and relationship of the child with their parent differ, and so we would expect attachment styles to vary as well. The attachment style towards romantic partners, friends, and other members of society would also require a different relationship, and possibly a different style of attachment. It seems that at each developmental stage, one would want or need different things from the relationship, so the same attachment style might not always be appropriate.

On the other hand, there are also reasons to expect some degree of stability in attachment styles over time. For example, Del Giudice addresses genetic influences on attachment styles during the course of development, but fails to properly discuss genetic predispositions (e.g., temperament) of the child which might be present at birth, thus setting a baseline on which to build during development. Del Giudice partially addresses the stability of attachment style over time, but does not suggest which factors might differentially influence those individuals who do and who do not have stable attachment styles over time, given the probable existence of such predispositions.

As Del Giudice is aware, our laboratory has published multivariate models of latent life-history constructs that support the cross-situational consistency of attachment styles across both childhood attachment to parents and adult attachment to romantic partners (Figueredo et al. 2004; 2006; 2007). This latent variable has been shown to have a high heritability coefficient ($h^2 = .65$) and is probably a good candidate both for early childhood predispositions that shape later developments and an individual difference variable that predicts temporal stability versus instability in attachment styles over time. Although Del Giudice cites this work, he does not pursue its implications for the resolution of this theoretical problem.

There are also various miscellaneous concerns to which we would have liked Del Giudice to respond. For example, we disagree with the statement (in sect. 3.1, para. 2) where Del Giudice writes, "In order to be selected for, traits need to solve two problems: being adaptive at the present time and being adaptive in the future of the organism." Selection has nothing to do with the future of the individual organism. It has to do with what worked in the ancestral past (teleonomy). Does the author understand this principle, or is this just a very poorly worded sentence?

We are also confused by Del Giudice's analysis of polygyny and attachment. We can understand how the arguments apply to serial polygyny, where the father ends one relationship and moves on to another one, potentially decreasing the resources invested in the previous family. However, we do not understand how this relates to societies with simultaneous polygyny, where the father will continue to invest in previous wives/families, even if it is only through material resources rather than bioenergetic ones.

Despite our criticism of the target article, we do feel that it is important to make the issue of evolutionary bases for sex differences known to a wider audience. However, in its present execution, the article seems to be lacking in ability to resolve some of the key issues concerning this topic.

Evolution of neuroendocrine mechanisms linking attachment and life history: The social neuroendocrinology of middle childhood

doi:10.1017/S0140525X09000089

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Abstract: An extended period of childhood and juvenility is a distinctive aspect of human life history. This stage appears to be important for learning cultural, social, and ecological skills that help prepare the child for the adult socio-competitive environment. The unusual pattern of adrenarche in humans (and chimpanzees) may facilitate adaptive modification of the neurobiological mechanisms that underpin reproductive strategies. Longitudinal monitoring of DHEA/S in naturalistic context could provide important new insights into these aspects of child development.

Living organisms are flexible; they can respond to changing conditions with a variety of morphological, physiological, and behavioral mechanisms. The processes that organisms use to change and respond to environmental challenges are posited to be evolved adaptations (West-Eberhard 2003). The development of the psychology of the human child may be viewed as a complex set of flexible adaptations (Bjorklund & Pellegrini 2002). Del Giudice proposes a comprehensive model for how humans might adjust future reproductive strategies – such as timing of puberty, mate choice, and parental behavior – in response to environmental conditions during middle childhood. His ideas are exciting because they suggest new research directions, including investigation of the stimuli that affect release of adrenal androgens (DHEA/S), and the associated effects on neurobiological development.

The human child must master the dynamics of social networks and culture, supported by the extraordinary information-processing capacities of the human brain (Adolphs 2003; Roth & Dicke 2005). We are interested in the unusual sensitivity of the fetus and child to the social environment – interpersonal relationships – and the consequent changes that occur in neuroendocrine systems. Our curiosity is piqued by both the paradoxical nature of this phenomenon – for some hormonal responses have attendant somatic costs (e.g., Flinn 2006; Muehlenbein & Bribiescas 2005) – and its importance for human health. For example, maternal depression and high levels of social anxiety during pregnancy are associated with low birth weight, elevated stress reactivity, and subsequent disease risk for offspring (Barker 1998; Gluckman & Hanson 2006; Weinstock 2005). The processes that underlay this biological embedding of information from the social environment in humans remain obscure.

On the basis of life history theory, the delayed reproductive maturity represented by an extended period of childhood and juvenility in humans is predicted to be important for learning cultural, social, and ecological skills that help prepare the child for the adult socio-competitive environment (Flinn et al. 2005; Geary & Bjorklund 2000). During this developmental period, boys and girls show behavioral sex differences in play and social interactions: boys tend to invest more time in organizing groups of peers, among which they form hierarchies, and compete with other groups. Conversely, girls usually invest more time in dyadic interactions with similar-age girls, caring for siblings, and doing domestic chores (Geary & Flinn 2002; Quinlan et al. 2003). How the onset of male coalitional and female dyadic psychobiology and life history trajectories might be influenced by family environment is yet an open question.

In the target article, Del Giudice draws our attention to the life history stage of middle childhood, which has not received much attention in comparison with infancy and early childhood on the one hand, and adolescence and the transition to early adulthood on the other. Yet it is childhood that distinguishes humans from other primates (Bogin 1999), and it is the period during which some of the most uniquely human socio-cognitive abilities are developed and refined (Geary 2005b). Adrenarche appears to be a key neuroendocrine transition in middle childhood that may facilitate the ontogeny of the neural mechanisms that underpin human sociality (Campbell 2006). Humans (and chimpanzees), moreover, have an unusual pattern to adrenarche. A few months after birth, the fetal zone of the adrenal cortex disappears and the levels of DHEA(S) diminish to near zero. In other primates, such as macaques and baboons (Muehlenbein et al. 2003; Nguyen & Conley 2008), newborns have high levels of DHEA(S) (compared to chimpanzees and humans) that slowly and steadily decrease with age.

In humans, adrenarche typically begins around age 7 years for females and 9 years for males (Dhom 1973), and DHEAS levels peak earlier in females than in males (Orentreich et al. 1984; Sulcova et al. 1997). The zona reticularis of the adrenal gland gradually begins developing at around age 3 years, at which time the production of DHEA(S) begins (Palmert et al. 2001; Remer et al. 2005). DHEA(S) is produced by the adrenal gland and converted to DHEA within target cells (Labrie et al. 1998). DHEA can then be converted into other androgens, such as androstenedione, as well as estrogens. DHEA acts antagonistically to cortisol (Hennebert et al. 2007; Kimonides et al. 1999), and both are derived from the pregnenolone precursor (Rainey et al. 2002). Timing of adrenarche also appears to be sensitive to environmental conditions; low-quality parental investment predicts earlier onset of adrenarche (Ellis & Essex 2007). Infants with a lower birth weight also exhibit earlier age at adrenarche (Ong et al. 2004).

The links between adrenarche and the socio-cognitive demands of middle childhood are uncertain. Androgens associated with adrenarche are likely important for brain maturation (Campbell 2006). DHEA(S) is a neurosteroid expressed in the developing brain in a region-specific fashion and involved in regulating the organization of the neocortex (Compagnone & Mellon 1998). While brain growth in humans is almost complete by age 7 years (the typical time of onset of adrenarche), cortical maturation with synaptic pruning continues (Gogtay et al. 2004). Glucose metabolism rates in the brain also remain high until around age 10 years (Chugani et al. 1998). DHEA(S) promotes neurological functions in rodents (Karishma & Herbert 2002), and DHEA(S) binds to various receptors in the human brain, including GABAa (Majewska et al. 1990). DHEA(S) may also affect mood in humans (Arlt et al. 2000; Micheal et al. 2000).

Functional connections between the middle childhood attachment transitions and adrenarche, however, remain speculative; the timing could be coincidental. DHEA(S) production has several physiological roles in childhood, including muscle and bone growth (Zemel & Katz 1986) and immuno-stimulation (Chen & Parker 2004). Rises in DHEA(S) during adrenarche may also be important in the hypothalamic desensitization associated with the onset of puberty (Tanner 1978).

"Attachment" in humans appears to involve additional functions beyond security and protection; the flow of information from parents and other relatives, and recruitment into kin-based coalitions, emerge as critical challenges for the child. Predicting what one's social environment will be as an adult and modifying phenotypic trajectories of the hormonal, neurological, and psychological mechanisms that comprise "internal working models" seems extraordinarily complex, and unlikely to favor early canalization of reproductive strategy. A more flexible system that allows inclusion of input throughout childhood and adolescence would have advantages over one primarily contingent on conditions during infancy (cf. Belsky 2002; Draper & Harpending 1982; Quinlan & Flinn 2003).

To evaluate the exciting new ideas about the adjustment of reproductive strategies in middle childhood proposed by Del Giudice, it would be useful to have research designed to specifically evaluate causal relations among the key proximate mechanisms. Comparisons with other primates will help identify what aspects of human adrenarche are shared or derived. Analyses of patterns of attachment and adrenarche in apes would be most interesting. Longitudinal studies of human child development that monitor DHEA(S) levels in naturalistic context could provide detailed data on links among hormone levels, family environment, affiliative bonds, and long-term outcome measures.

Attachment strategies across sex, ontogeny, and relationship type

doi:10.1017/S0140525X09000090

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Abstract: We propose that middle childhood female ambivalent attachment, given the adaptive problem of uncertainty of future investment, is designed to evoke immediate investment from current caregivers, rather than new investment sources. We suggest greater specificity of strategic attachment solutions to adaptive problems that differ by sex, time, and relationship type.

The target article represents a major theoretical contribution on several fronts. First, it highlights evolutionary functional accounts as indispensable for any comprehensive theory of attachment (as initially envisioned by Bowlby [1969/1982], but neglected by many subsequent attachment theorists). Second, it focuses on sex differences in adaptive problems and the resultant attachment-related strategic solutions as males and females enter the arena of mate competition. And third, it provides an elegant theoretical integration of the evolutionary psychological work on sex differences in mating strategies with important dimensions of individual differences – something urgently needed, but relatively neglected by much previous work in evolutionary psychology (Buss & Greiling 1999). In this commentary, we build upon these important advances, and propose some directions for exploring additional attachment differences across time, sex, and adaptive problem domain.

Evolution by selection tends to produce domain-specific and context-specific adaptations. It is theoretically problematic to assume that the attachment strategy as an adaptive response to environmental cues at one point during development will be adaptive if implemented in interactions in relationships later in life. To the degree that mother–infant attachment bonds serve functions that differ from those of friendship bonds and mateship bonds, and to the degree that they differ by sex, we expect selection to favor specificity of strategic solutions by relationship type, sex, and life phase.

It is reasonable to hypothesize that the sex differences in relative frequencies of insecure attachment styles that emerge at middle childhood are a result of sex differences in adaptive problems faced recurrently over deep evolutionary time during this stage of development. Del Giudice provides a compelling functional account for the shift in males towards an avoidant attachment style, but notes that the function of the female skew towards an ambivalent attachment style at this age is "less clear" (sect. 7.1.2, para. 2). If we focus on the finding that girls of parents who provide only inconsistent and unpredictable investment are the ones who tend to develop ambivalent attachment styles, we can conceptualize their ambivalent attachment psychology during middle childhood as a solution to the adaptive problems predicted by their parent-specific and kin-specific input.

The ambivalent attachment style is characterized by extreme dependence, emotional instability, and a desire to exert influence over the caregiver (sect. 2.2). These strategies, perhaps effective in eliciting as much investment as possible from parents, are unlikely to succeed in establishing strong alloparental bonds if directed toward same-sex peers during middle childhood. There is evidence that female–female friendships during childhood are shorter and more fragile than male–male friendships (Benenson & Christakos 2003). If female friendships at this age lack the stability to endure until reproductive age, it strains credulity that they function as precursors to lasting alloparental bonds. Exhibiting high dependence and emotional instability toward female friends could easily backfire, as mechanisms that caused individuals to invest in non-kin who deplete resources, but who are unable or unlikely to reciprocate, would be selected against (Trivers 1971). From this perspective, we would not predict that attitudes and characteristics associated with ambivalent attachment at middle childhood would result in behavior that successfully initiates or maintains same-sex peer relationships.

If we instead hypothesize that this strategy is designed to be directed towards parents or kin, a functional hypothesis presents itself. In an environment in which male parental investment is inconsistent or nonexistent, such as that associated with ambivalent attachment, females who waited longer to reproduce, or who attempted to obtain all the necessary investment from their future mate, would have been out-competed by females who began reproducing early and who attempted to extract resources and investment from kin (Belsky 1997a; 1999; Hoier 2003; Quinlan 2003). Moreover, the earlier a female reproduces, the more likely she is to receive grandparental assistance and resources. Given cues to low or unstable male parental investment, one adaptive solution would be to reproduce early and maintain high levels of dependence upon close kin.

Because kin are usually already invested in the survival and reproductive success of their genetic relatives, we hypothesize that the care-eliciting strategies associated with ambivalent attachment directed specifically toward kin have the best chance of successfully extracting investment for a female's offspring. In contrast, similar strategies directed toward peers may result in alienation. In an environment in which male parental investment is unreliable or unlikely to be forthcoming, reproducing early capitalizes on as much grandparental investment as possible while these extended kin are still alive and can invest. Whereas securely attached individuals expect consistent support from family members, insecurely attached females may do best to focus on obtaining as much support as possible during middle childhood, because they cannot rely on it for the future.

Building on the theoretical advances proposed by Del Giudice, we have focused on functional explanations for the female switch to ambivalent attachment patterns during middle childhood. We suggest that this domain-specific approach will yield a psychological harvest for each sex, life stage, and relationship type. To the degree that sex-specific adaptive problems are associated with different types of dyads such as mateships, friendships, and kinships, we expect that selection will favor sex-specific, relationship-specific, and life-stage-specific strategic solutions.

Co-regulation of stress in uterus and during early infancy mediates early programming of gender differences in attachment styles: Evolutionary, genetic, and endocrinal perspectives

doi:10.1017/S0140525X09000107

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Abstract: According to evolutionary, genetic, and endocrinal perspectives, gender differences are modulated by the interaction between intra-uterine stress, genetic equipments, and the availability of the facilitating environment during the newborn period. The social message of fitness over obstacles during socialization and the discussion of secure/non-secure attachment styles should take into consideration the brain functions, which are altered differently in response to intra- and extra-uterine stress in each gender.

Sexual selection is governed by social selection, and social regulation should also be taken into account. The "helper" hypothesis raised by Del Giudice is exactly this kind of mechanism. Del Giudice's characterization of the stress-stricken male as being more aggressive, more dominant, and more competitive may be considered as the early selection of boys to raise the cutoff point of survival, leaving only the highly fit individuals for adult stages when same-sex competition determines the odds for reproduction. This is buttressed by a series of studies in the obstetric literature from this decade, indicating the greater vulnerability of male fetuses as compared to female fetuses (Anderson & Doyle 2008; Deulofeut et al. 2007; Ingemarsson 2003; Jones et al. 2005; Pressler & Hepworth 2002).

Evolutionary logic may also explain the observed phenomenon. Ingemarson (2003) offers a view of the fetus as basically female. The masculinization process is regarded as an excess process that brings an additional set of risks to the fetuses' development. This could be interpreted similarly to the evolutionary Handicap Principal, according to which, excessive survival risks characterizing animals convey a social message of fitness over obstacles (Cellerino & Jannini 2005).

It may be argued that males have a genetic disadvantage because they are equipped with two distinct sex determination chromosomes (XY) instead of the parity backup that exists in females, who have two of the same kind of sex determination chromosomes (XX). Ingemarsson (2003) claims that in comparison with the X chromosome, the Y chromosome has degenerated through evolution and includes only a small number of genes, all of which are heterozygote. Having only one copy of each gene means that every "bad" allele is expressed.

A mediating factor for the gender genetic differences may be stress (Als 1986; Als et al. 1994; 2004; Heckman et al. 2005). Phillips (2007) claims that antenatal stress has life-long effects that vary among men and women, and suggests the possibility of gender dimorphic environmental fetal programming. Davis and Emory (1995) show gender dimorphic stress reaction in healthy, full-term infants prior to extensive socialization.

Therefore, I suggest that these differences found in the response to stress are constructed and programmed in utero and continue to develop differently during the socialization process, so that the factor of stress, as suggested by Del Giudice, only secondarily affects gender differences, interacting after birth with this early programming. Meaney and Szyf (2005) examined this issue with an animal model and found that increased levels of pup licking/grooming by rat mothers in the first week of life alter the DNA structure at a glucocorticoid receptor gene promoter in the hippocampus of the offspring. These effects are far more robust in females, suggesting that girls may be better equipped genetically but may also have a greater vulnerability to non-supportive environmental signals, and that this is the manner in which the non-secure girl develops an anxious attachment style, as claimed by Del Giudice.

Findings from Francis et al.'s (2002) animal studies are in accordance with the above. Francis et al. found that in the central nucleus of the amygdala and bed nucleus of the stria terminalis (which encompasses discrete, anatomically separate populations of oxytocin and vasopressin receptors; Huber et al. 2005), oxytocine receptors binding – which decreases anxiety and stress, and facilitates social encounters, maternal care, and the extinction of conditioned avoidance behavior – was increased in adult females, but not adult males, that had received high levels of maternal licking and grooming as pups. Conversely, amygdala vasopressin receptor binding – which is involved in modulating fear and aggression – was increased in males, but not females, that had received high levels of maternal licking and grooming. This further explains the manner in which the non-secure boy, in order to appear robust in the environment, develops – as suggested by Del Giudice – an avoidant attachment style.

The attachment styles may be understood not as gender differences so much as differences in the gender construct of society and its interaction with the genetic fetal equipment for dealing with intra- and extra-uterine stress, leading female offspring to be better fitted to deal with social pressure by seeking bonding and male offspring to be better fitted to deal with social pressure by avoiding collision. Therefore, finally, the gender effect could be explained by socialization: It could be that mothers care for boys and girls differently, according to certain social gender roles, as well as certain cues coming from the infant which are already formatted in utero.

The social context of my assumptions suggests that the interplay of sex hormones and stresses is an interfering factor in the aromatization process of masculinization, whereas Del Giudice refers to sex hormones as mitigating stress. In the face of contradicting results and theories, the concept of *co-regulation* may be considered (Als 1986; Goldstein Ferber 2008; Hofer 1994). That is, in situations of good co-regulation between neurobehavioral subsystems in utero and in the newborn period, a boy may benefit from the interplay between these subsystems, including the development of the sex hormones; whereas, in cases where such a co-regulation state is lacking, especially in the deregulation of the development of the hypothalamic-pituitary-adrenal (HPA) responses, the interplay may turn into an interfering process and result in difficulties as early as during gestation.

Additional perspectives suggest that within a regulatory process in early parental interactions, with the offspring's cues already shaped in utero, the dyadic reciprocal regulation between the child and his or her parents in these early interactions (Archer 1996; Cho et al. 2007) may determine (1) whether the boy or the girl develops a secure attachment style, and (2) whether the boy or the girl develops his or her gender's typical disadvantage in attachment style (i.e., either avoidant or anxious).

Therefore, I suggest that the level of fitness between the gender-type cues shaped during gestation, the ability of the parents to reciprocate with those cues, and the social interest the parent represents, work in feedback circuits. Having said that, it seems that socialization and the development of attachment styles are processes provided with windows of opportunities during critical ages in early childhood, and that anthromorphologic structural theories are able to explain contradicting research data by functional ante- and postnatal processes.

Attachment theory underestimates the child

doi:10.1017/S0140525X09000119

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Abstract: The problem with elaborations of attachment theory is attachment theory itself. How would a mind that works the way the theory posits have increased its owner's fitness in hunter-gatherer times? The child's mind is more capacious and discerning than attachment theorists give it credit for. Early-appearing, long-lasting personality characteristics, often mistaken for the lingering effects of early experiences, are more likely due to genetic influences on personality.

The human mind was shaped by natural selection. The mind we inherited from our ancestors was tested against alternative versions and won out against the competition because it was more successful in dealing with the challenges of hunter-gatherer life. Would the mind depicted by attachment theorists have passed this test? Would it have helped its owner survive and reproduce in the Paleolithic?

According to attachment theory, an infant develops expectations about the world and its people on the basis of the way his mother takes care of him. How would this be beneficial to him? Why should a child with an attentive mother expect other people – siblings, peers, strangers – to be equally attentive? And how would it profit the child of a negligent mother to go into the world with the expectation that no one will love him? Isn't the child's mind capacious enough to form separate "working models" for all the important people in his life, so that he can behave appropriately with each of them?

According to the "life history" elaboration of attachment theory, a girl who experiences a stressful environment in the first few years of life, or whose father was absent or insufficiently attentive during that period, is more likely to reach sexual maturity early and to hasten into sexual relationships with temporary partners. But didn't every child grow up in a stressful environment in the Paleolithic? Many parents died before their children were grown. Polygyny was probably universal, limited only by men's ability to support additional wives. As noted in the target article, paternal childcare is rare in polygynous societies.

According to life history theorists, the child's experiences with parents in infancy and early childhood influence her reproductive strategy 10 or 12 years later. But why should a girl's reproductive strategy be based on such inadequate data? Many things might change in the interim, so why not wait as long as possible to settle on a strategy? And why look only at her own parents? Birds are capable of making a decision about next year's nesting site on the basis of "public information" they collect by observing other nests in the area (Doligez et al. 2002). If a bird can do it, why not a child? Her family may be atypical, so the more data she collects the better.

Attachment theory underrates the child. There is good evidence that children construct separate working models for each of the important people in their lives, and that expectations developed in one relationship are not carried over to other relationships. Babies can be securely attached to one caregiver and insecurely attached to another. Infants of depressed mothers are subdued with their mothers but behave normally with other familiar caregivers. Children who are pushed around by older siblings at home are fully capable of taking a dominant role with peers (see Harris 1998; 2006).

Although behavior is highly sensitive to context, it is not ruled solely by context. Researchers observed children interacting with their parents and the same children interacting with their peers, and recorded instances of uncooperative, angry, or bossy behavior. The correlation between behavior with parents and behavior with peers was .19 (Dishion et al. 1994). I attribute this correlation not to generalization or transfer but to heritable personality traits (e.g., disagreeableness) that the child takes along to every social context. Confirmation comes from behavioral genetic studies of other behaviors, such as shyness. Correlations between shy (or bold) behavior in two different contexts are almost entirely due to genetic influences on these behaviors. In contrast, environmental influences on shyness are context-specific (Saudino 1997).

The same holds true for consistency over time. The long-term stability of personality traits is primarily due to the heritable component of such traits (Caspi & Roberts 2001). This finding has an important implication: Personality characteristics that appear early in development and persist into adulthood are largely genetic and not, as most developmental psychologists have assumed, due to the lingering effects of early experiences.

Though the role of genes in producing resemblances between siblings is now generally acknowledged, the fact that children also share half their genes with their biological parents – *both* parents – is widely ignored. For genetic reasons alone, people who are impulsive, quickly bored, easily angered, or prone to depression have a greater-than-average risk of producing offspring with similar disadvantages. A pretest for temperament in infancy is a hopelessly inadequate way to control for genetic influences on behaviors measured in infant, child, and adult attachment tests (Rowe 2000b).

Attachment theory is based almost exclusively on studies that examine one child per household; almost always, the child is the biological offspring of the mother. This method makes it impossible to disentangle environmental and genetic influences. Studies of twins, siblings, and adoptees – two per household – have shown that about half the variance in most psychological characteristics can be attributed to genetic influences, and most of the remainder to unknown "unique" influences (see Harris 2006). The environment shared by children who grow up in the same household accounts for little or none of the variance. Physical maturation – age at menarche – follows the same pattern; although heritability is higher, most studies find little effect of shared environment (see Mendle et al. 2006). Whether or not a father is present, and whether or not the home is stressful, are aspects of the shared environment.

As Nettle (2006) has argued, most individual differences in mating behavior can be attributed to heritable personality characteristics. Differences in rate of maturation are also heritable, and the environmental factors that play a role may not be the ones discussed in the target article. For instance, the role of socioeconomic status (SES) is often overlooked. Girls in troubled households may mature more rapidly because, in developed nations, obesity is negatively correlated with SES: children in lower-SES homes and neighborhoods tend to be fatter (Shrewsbury & Wardle 2008). Because age at menarche depends on body weight, overweight girls mature faster (Frisch 1988). The link between body weight and rate of maturation can also explain why girls today are maturing faster than they used to (Cesario & Hughes 2007). The increased prevalence of obesity is probably to blame.

In conclusion, correlations between infant attachment behaviors and later sexual relationships are most likely due to persisting, heritable personality traits. Evolutionary psychologists and biologists can explain sex differences in sexual relationships without recourse to attachment theory.

Pre-adjustment of adult attachment style to extrinsic risk levels via early attachment style is neither specific, nor reliable, nor effective, and is thus not an adaptation

doi:10.1017/S0140525X09000120

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Abstract: The mechanism proposed by Del Giudice by which adult attachment style is adapted to the extrinsic risk in the local environment via attachment style during the early years does not fulfill important criteria of an adaptation. The proposed mechanism is neither specific, nor developmentally reliable, nor effective. Therefore, it should not be considered an adaptation.

In the wake of similar models (Belsky et al. 1991; Chisholm 1993; 1996; 1999), Del Giudice proposes an adaptation consisting of multiple steps that adapt adults' attachment style and reproductive strategy to the level of extrinsic risk in their local environment via their attachment style during early years. Unfortunately, Del Giudice never discusses which criteria we should use to establish if a certain mechanism or structure is an adaptation. Andrews et al.'s (2002) summary of the debate on this issue shows that specificity, developmental reliability, and efficiency figure prominently among these criteria. The mechanism envisaged by Del Giudice fails on all three of them.

Although parental behavior has a moderate effect on children's attachment style (De Wolff & van IJzendoorn 1997), the latter appears to be insensitive to the extrinsic risk of the environment. In a cross-cultural review of attachment patterns, van IJzendoorn and Sagi (1999) find one of the highest proportions of secure attachment (88% with a tripartite coding system) in the Dogon, for which child mortality is extraordinarily high (25% of children die within their first five years). Thus, deviation from secure attachment does not appear to be very sensitive to extrinsic risk. In addition, unusually high deviations from secure attachment were found in kibbutz children (31% to 52% not securely attached). But the reason for this high level of insecure attachment is not an extrinsically risky environment but, rather, that infants sleep away from their parents, with Israeli day-care infants showing secure attachment rates between 75% and 80%. Thus, the effect of extrinsic risk on infant attachment style lacks specificity because risk hardly (if at all) affects attachment style, whereas an irrelevant variable (sleeping away from parents) has a strong effect on attachment style.

However, even if the proportion of non-securely attached children clearly covaried with the extrinsic risk of the environment, the overall low variability in the relative frequency of attachment patterns should be noted. Van IJzendoorn and Sagi's (1999) review strongly suggests that secure attachment is the norm across very different environments. If deviation from secure attachment were adaptive in the face of high extrinsic risk, we would thus find that the majority of children in cultures that suffer from high childhood mortality or other high risks are maladapted because they are securely attached. However, if deviation from secure attachment were adaptive under these circumstances, we should observe developmental reliability; that is, the shift away from secure attachment should be ubiquitous and not only seen in a fraction of children. Women's esthetic judgment of male bodies may serve as an example for the ubiquity of an alleged psychological adaptation in humans. Hönekopp et al. (2007) hypothesized that women evolved an adaptive preference for the bodies of athletic men. In line with the notion that an adaptation should be developmentally reliable, a preference for the bodies of athletic men was found for all women in their sample.

Even if the mechanism envisaged by Del Giudice were specific and developmentally reliable, it would still be unlikely to be effective. The reason is that the proposed chain of information transmission is simply too long: In the ideal case, a match between A's reproductive strategy and the extrinsic risk of the environment would come about because (1) the risk during A's adulthood correlates with the risk during A's early years, (2) the risk during A's early years correlates with A's parents' care-giving behavior, (3) A's parents' care-giving behavior correlates with A's early attachment style, and (4) A's early attachment style correlates with A's adult attachment style and reproductive strategy. Even if we assume an unusually high correlation of $r = .7$ within each of the four links, half of the relevant information would be lost during each transmission stage (because two variables that correlate with $r = .7$ have $0.7^2 = 49\%$ variance in common). This information loss multiplies over the whole chain, so that 94% of the relevant information is lost at the end of the chain ($1 - \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}$). Of course, even a mechanism that loses 94% of the relevant information may be adaptive if there is no better alternative. But obviously, A has ample opportunity to directly observe the extrinsic risk in the local environment. As humans' sexual strategies appear flexible enough to take such information into account (Gangestad & Simpson 2000), A's mating strategy should be based on the observation of the current environment. And the availability of this more direct strategy renders the mechanism proposed by Del Giudice utterly ineffective.

In sum, the proposed mechanism of adjusting adult romantic attachment style and sexual strategy to the extrinsic risk level of the local environment via attachment style during the early years lacks specificity, developmental reliability, and efficiency, and should therefore not be considered an adaptation.

Synthesizing life history theory with sexual selection: Toward a comprehensive model of alternative reproductive strategies

doi:10.1017/S0140525X09000132

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Abstract: Del Giudice's model of sex-specific attachment patterns demonstrates the usefulness of infusing life history theory with principles of sexual selection. We believe a full synthesis between the two theories provides a foundation for a comprehensive model of alternative reproductive strategies. We extend Del Giudice's ideas based on our own program of research, focusing specifically on the importance of intrasexual competition and the individual phenotype during development.

Del Giudice's explication of sex-specific patterns of insecure attachment substantively advances our understanding of attachment organization across development and its role in shaping adult reproductive strategies. An important strength of the model is the incorporation of parental investment and sexual selection theory into current life history models, enabling a better account of sex-differentiated life histories. The focus on sex-specific reorganization of attachment patterns in middle childhood as a critical phase in the formation of reproductive strategies is a novel and exciting idea that should stimulate future research.

Despite these strengths, the synthesis of life history theory and sexual selection theory needs further development. A comprehensive model must incorporate not only the concept of asymmetries in parental investment between the sexes, but also the alternative reproductive strategies that arise within each sex as a result of intrasexual competition. Current sexual selection models, such as Gangestad and Simpson's Strategic Pluralism

Theory (2000), emphasize social and sexual competition as important factors shaping adaptive variation in reproductive strategies.

The incorporation of ideas from sexual selection theory into life history models should be especially valuable because the weakness of one theory is often the strength of the other. For instance, life history theory has provided the basis for a useful set of models for explaining development of variation in women's reproductive strategies (e.g., explaining developmental trade-offs between current vs. future reproduction; see Belsky et al. 1991; Ellis 2004). However, because life history models have not adequately addressed social-sexual competition for mates, they have been limited in their ability to explain strategic variation among men. Sexual selection models, by contrast, have been successful in explaining how males apportion reproductive effort to mating versus parenting in relation to current levels of social-sexual competitiveness (e.g., Gangestad & Simpson 2000; Gross 1996), but do not provide an adequate developmental model for how and when males should make these adaptive shifts.

To address these limitations, we have constructed a more comprehensive theoretical framework based on the strengths of each model (Jackson & Ellis, submitted; Jackson et al., submitted). Our approach toward this synthesis has been to integrate the components of social and sexual competition into the developmental trajectories laid out by life history theorists. Our theory and research in this area focus on how early familial environments and status obtained in adolescence and early adulthood contribute, additively and in interaction, to the development of reproductive strategies in men and women.

Because males and females must solve qualitatively different adaptive problems when negotiating life history trade-offs, there should be important sex differences in the tracking of environmental information, or at least the weight given to specific environmental cues (see Gangestad & Simpson 2000; Thiessen 1994). Females are ultimately constrained by the resources that they can extract from the environment, their relatives, and their mates in order to successfully produce and rear offspring; accordingly, they should be especially attuned to the nature of the local ecology and support in and around their home environments, per life history models. Males, on the other hand, are ultimately constrained by their ability to access, attract, and retain females; accordingly, their own reproductive strategies should be especially attuned to the demands and desires of females and their ability to successfully engage in intrasexual competition, per sexual selection models.

Recent empirical studies lend support to these claims. In a longitudinal study on adolescent development, Ellis and Garber (2000) found that early psychosocial stress (i.e., discordant family relationships, father absence/stepfather presence) predicted early pubertal maturation among girls. In the same sample, Jackson et al. (submitted) examined the effects of early psychosocial stress within the home and competency within the peer group on attachment orientation and sexual behavior in late adolescence. As in the previous analyses of pubertal timing, in females, but not in males, early psychosocial stress was a reliable predictor of heightened sexual activity, risky forms of sexual behavior, and avoidant romantic attachment patterns. By contrast, in males, but not females, self-perceived social competence and athletic ability during adolescence were reliable predictors of heightened sexual activity and secure romantic attachment in late adolescence. Thus, consistent with our model, development of female reproductive strategies was more closely linked to variation in familial and ecological conditions, whereas development of male reproductive strategies was more closely linked to social-competitive ability and status.

All children do not respond equally, however, to family environments and social-sexual competition. An important factor noted in section 6.4, but not explicitly modeled by Del Giudice, is that the effects of attachment on social and reproductive strategies may depend on the phenotype of the developing child. Phenotypic characteristics likely moderate the developmental pathways presented by Del Giudice in the following ways. Among females, phenotypic quality could alter the extent to which they are able to extract resources from relatives and mates, moderating in part the relationship between extrinsic risk, attachment orientation, and sexual behavior in adulthood. Among males, phenotypic quality could alter the extent to which they are able to enact specific competitive and reproductive strategies. For instance, the male avoidant strategy detailed by Del Giudice includes a personality profile of inflated self-esteem, self-reliance, and aggression that facilitates status seeking. Although we agree that these traits may aid in intrasexual competition in certain social niches, it is likely that only those males who possess the physical prowess needed to successfully compete in such a manner would benefit from the strategy. Along these lines, Figueredo and Jacobs (2000) have argued for a kind of reactive heritability model whereby the inheritance of strategically relevant traits biases individuals toward different strategies. They contend that, "psychosexual development involves a self-assessment of sociosexual capabilities and opportunities, calibrating optimal utilization of physical assets such as size, strength, health, and attractiveness, as well as psychosocial assets such as intelligence, self-efficacy, social skills, personality, and socioeconomic status and/or prospects" (p. 603). In sum, extant phenotypic characteristics should interact with social status and developmental experience to determine life history strategies.

In conclusion, Del Giudice's ideas concerning the sex-specific organization of attachment beginning in middle childhood are likely to assume an important role in research on development of life history strategies. We see Del Giudice's model, together with our own, as affording meaningful steps toward the integration of life history and sexual selection models of human reproductive strategies.

Attachment patterns of homeless youth: Choices of stress and confusion

doi:10.1017/S0140525X09000144

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Abstract: This commentary explores the reproductive strategies and attachment patterns among homeless youths. Del Giudice's integrated evolutionary model is applied to a homeless youth population that must function in ecological settings of constant high risk and stress. Different reproductive needs result in different patterns of high-risk behaviors. Intervention considering the sex differences, life history, and early caregiver–child relationships is suggested.

It is difficult to imagine situations with higher levels of stress and greater relative extrinsic dangers than those faced by homeless youth on a given day. There are between 500,000 and two million homeless youth in the United States (Cooper 2006), with few social service or non-governmental agencies to help them (Wright 1990). Homeless youth have a number of hygiene and health vulnerabilities that make them outcasts in society (Staller 2004); but they also tend to avoid and be mistrustful of what society might have to offer. Del Giudice's target article informs the issue of homeless youths in two ways: (1) it offers insight into what we believe to be the extreme avoidant behavior of many homeless youths, especially males, and (2) it provides a possible context for many of their behavioral choices, especially those pertaining to sexuality and reproduction. Del Giudice's thesis examining the interconnection between attachment patterns, life histories, and reproductive strategies allows us to view the extreme avoidant behavior, and seemingly illogical reproductive choices (e.g., young girls having children with transient partners while they are homeless), through the lens of an adaptive model rather than a deficit model; except, it is adaptation turned on its head by brutal and uncaring social ecologies.

Many homeless youth begin to engage in sexual activity at an early age – sometimes as the result of relationships and sometimes as a means to an end (survival sex). Del Giudice's reference to Sroufe et al. (1993) concerning the intersection between life stress, insecure attachment patterns, and early violation of gender boundaries in middle childhood has particular resonance. A number of youths seem to become highly sexualized in their behavior relatively early in life, with flirtation becoming a dominant form of communication and connectivity. For males, flirtation and early sexual behavior are part of the initiation into the same-sex social hierarchy that will eventually determine their place in the street economy. The need to develop an avoidant stance towards relationships is critical.

The females may be more confused about what their flirtation means. A number of homeless females have been sexually abused, been raped at some point, or used sex for survival purposes. At the same time, flirtation and sex through middle childhood and into adolescence is one of their surest relational strategies.

When homeless youth do engage in sex, many times it is unprotected, leading to both pregnancy and the spread of sexually transmitted diseases (STDs). Although this may seem like foolish or self-destructive activity to a casual observer, Del Giudice's thesis suggests that these youths are following natural reproductive strategies that meet needs determined by their circumstances. Many of the males will meet violent ends, become alienated homeless adults, or wind up in jail. There is a drive to impregnate females while remaining distant. The females are often left alone with children while they are still homeless or living on the margins of society, leading them to exhibit depressive symptoms (Meadows-Oliver 2007). Research has suggested that depressed mothers who have low emotional availability (e.g., are less sensitive, less structuring, and more intrusive and hostile) during the early years of child rearing, tend to have children with low emotional availability (e.g., less responsive, less involving) (Easterbrooks et al. 2000). And this quality of emotional interaction can lead the insecure attachment patterns (Ziv et al. 2000), perpetuating a cycle of avoidance and alienation.

Stress becomes a regular part of the developing child's life, and the impact of life histories on choices becomes more evident and more dominant, with somatic resources used primarily for survival. Because the street economy often plays a major role in the lives of homeless youth, many males move in the direction of highly avoidant insecure attachment patterns. To establish long-lasting relationships is in many ways to become more vulnerable. They understand that their transient relationships – the members of their "posse" – are critical for their survival. On the other hand, many of the females who have been raised by single mothers understand that they represent the sole opportunity for their children to survive. They necessarily have to choose more ambivalent insecure attachment patterns to protect their child. However, once stress and/or extrinsic danger reaches such a high level that their attempts at caretaking strategies end in failure or prove to be impossible (for ambivalent homeless females' behavior choices don't so much involve "helping at the nest," as attempts to create a nest), their relationship strategies can change. We have seen a number of occasions where failure in attempts to develop a middle-class-type lifestyle (i.e., with job, stable living conditions) has caused once hopeful females to be even more avoidant and alienated than the males.

It is our hope that some of the ideas from Del Giudice's article might give us a better handle on the development of interventions for these homeless youth. To date, interventions have had only limited success, with one of the major impediments being lack of trust and extreme avoidant behavior. By focusing on reproductive strategies, we can hypothesize that one of the best times to engage female homeless youths is when they are pregnant. It is possible that this is the point at which they are most ready for and in need of establishing relationships, even if these relationships are based on ambivalent strategies. Unfortunately, the same phenomena that cause these females to want to establish linkages and relationships, make them highly vulnerable to failure or avoidance by society at large. If we can develop programs that are nonjudgmental and focused on success, especially involving "nesting" trajectories (e.g., getting stable housing that is not contingent and the resources necessary to raise a healthy child), there is the possibility of reinforcing lifetime linkages. And perhaps more importantly, it would allow these mothers to develop stronger, more emotionally available relationships with their children, breaking the cycle of depressive and self-destructive behavioral trajectories. Thus, an intervention that first helps the homeless females to successfully find the stability in housing, jobs, and social support, will reduce the chances of females being so passive in relation to males' reproductive strategies, leading to fewer opportunities for multi-mating (a major cause of paternal absence in parenting).

Developmental transformations in attachment in middle childhood

doi:10.1017/S0140525X09000156

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Abstract: The target article proposes a model to explain the emergence of sex differences in attachment in middle childhood and their implications for reproductive strategies. While biological factors are prominent in the model, little is said about the social context of middle childhood and its contributions. There is also a need to clarify the fundamental nature of attachment in middle childhood.

The Del Giudice target article raises important questions about how gender may play a role in the development of attachment in middle childhood. The author rightly notes that the influence of gender has been largely ignored in the attachment literature. The proposed model generates several novel hypotheses and is likely to lead to new research. Especially intriguing is the idea that insecure attachment may be reorganized differently for boys and girls in middle childhood in support of reproductive strategies that have evolutionary advantage.

Given that attachment theory is, in large part, a theory of social influence, it is surprising that the model does not specify the impact and role of social partners during middle childhood. The model depicts an "early experience" role for parenting, in which a parent's main role is to influence the initial development of attachment. Parents are, however, still the primary attachment figures for children in middle childhood (Kerns et al. 2006), which raises the question of what role they play in the proposed developmental transformation of attachment. For example, if a girl switches from an avoidant to a heightening strategy with a parent (as predicted by the model), presumably this would invoke some changes from the parent (e.g., increased rejection). The dyadic nature of parent–child relationships is not captured by the model. Relatedly, although peers play an important role in socializing gendered behaviors, very little is said regarding how peers may influence and amplify any emerging sex differentiation in attachment. Thus, while biological influences on attachment deserve greater consideration, the proposed model would be enhanced by also incorporating social influences in middle childhood.

A complexity in interpreting the model arises from the multiple meanings of the word "attachment." Does it refer to a child's relationship with a specific target, or to a child's general orientation (style) across different attachment relationships? Both meanings are used in the target article. There has been a lack of research on how experiences in multiple attachment relationships come to be integrated into a general orientation (e.g., "state of mind") to attachment. It is possible that this integration begins in middle childhood (Kerns et al. 2005), which may have some implications for the model. Specifically, the proposed sex-specific reorganization in insecure attachments could occur within the context of specific attachments (which would produce unstable relationships) or could be reflected in a child's (emerging) attachment style. It is possible that specific attachments may be influenced primarily by patterns of interaction with a partner, whereas attachment "style" is influenced by some combination of experiences in specific relationships, gender socialization, genetic propensities in personality traits, and evolutionary pressures for adaptive mating and reproduction strategies. If the author is correct in suggesting that the proposed sex differences in attachment are in the service of reproductive strategies, then it is also possible that sex differences in insecure attachment will be most pronounced in attachments to peers that develop in late adolescence (i.e., in relationships where mating and reproduction are more relevant).

A key prediction from the model is that, in middle childhood, most insecure boys will be avoidant, and most insecure girls will be ambivalent in their attachments. The literature review on gender differences in attachment, which was based on studies using doll play interviews or questionnaires, did provide evidence for sex differences in the distributions of insecure attachment in 6- to 12-year-old children. The review could have been more extensive. There are additional studies of this age range that have employed observational measures (e.g., Graham & Easterbrooks 2000; Moss et al. 2004) or autobiographical interviews (e.g., Ammaniti et al. 2000; Target et al. 2003) to assess attachment, but these studies were not included in the review. Evidence that sex differences are found using these other methods (as well as evidence for sex differences in Adult Attachment Interview [AAI] insecure classifications in adolescence) would provide stronger evidence that the pattern is not confounded with choice of methods. (Del Giudice's point about inattention to gender in the attachment literature is well taken, as most of the studies cited in this paragraph did not provide information regarding the sex breakdown within the insecure attachment groups.)

Interestingly, the review of studies also showed that many insecurely attached boys are disorganized. The author provides a cogent discussion of why insecure boys might be predisposed to adopt avoidant strategies; but why are so many boys in middle childhood disorganized in their attachments, and can this be accounted for by the model? Perhaps the model could be elaborated to identify factors in the social ecology (e.g., level of family stress) that might distinguish between boys who develop disorganized rather than avoidant attachments, but it is less clear how disorganized attachment might confer an adaptive advantage.

Despite these limitations, the article does generate many testable hypotheses, some of which are not intuitive and are not consistent with current theory. If there is a reorganization of insecure attachment in middle childhood that is not a result of changes in parenting, and an overall waning of the influence of parents, then presumably both cross-generational continuity in attachment (parent–child correspondence) and stability of child–parent attachment would be lower in middle childhood than in early childhood (although how much lower is not quite clear from the article). These corollary hypotheses are currently difficult to evaluate given the lack of relevant data (although see Target et al. [2003] for an exception). Longitudinal studies in early middle childhood are especially needed to test the hypothesis that girls and boys shift toward different insecure attachment patterns around age 7 years. Given the modest links between attachment and parenting in middle childhood (Kerns, in press), more elaborated models of the influences on attachment are needed. The model proposed by Del Giudice provides additional processes (specifically, biological mechanisms) that could be tested, as well as specifying how levels of stress may predispose girls and boys to different developmental pathways.

Life history as an integrative theoretical framework advancing the understanding of the attachment system

doi:10.1017/S0140525X09000168

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Abstract: Evolutionary Life History Theory (LHT) is a powerful framework that can be used for understanding behavioral strategies as contingent adaptations to environmental conditions. Del Giudice uses LHT as a foundation for describing the attachment process as an evolved psychological system which evaluates life conditions and chooses reproductive strategies appropriate in the developmental environment, integrating findings across several literatures.

Evolutionary Life History Theory (LHT) emerged in evolutionary biology (e.g., Pianka 1970) to describe the relationship between environmental conditions and reproductive patterns across species. The vast majority of research addressing LHT has been conducted in nonhuman species, and usually makes comparisons between species. In recent years, there has been a growing interest in human life history and life history variation within species (e.g., Heath & Hadley 1998). LHT holds great promise for promoting the understanding of our own species and integrating findings from diverse research methodologies spanning multiple levels of analyses.

Following the behavioral ecology principle that behavioral strategies related to reproductive success are conditional based on the characteristics of the physical, economic, and social environment (Crawford & Anderson 1989), Belsky et al. (1991) proposed that the attachment process is an evolved psychological system that evaluates life conditions and chooses reproductive strategies appropriate to the developmental environment. Del Giudice provides an overview of research related to this theory across a variety of perspectives and enhances its precision of prediction by adding insights from sex differences in human reproductive strategies. The target article, "Sex, attachment, and the development of reproductive strategies," demonstrates the value of LHT as a framework for integrating converging evidence across fields and levels of analyses to result in a more complete and comprehensive understanding of the complex factors underlying human behavioral patterns.

Evolution by natural and sexual selection is the most powerful theory in the life sciences, and in recent decades there has been considerable progress in using evolutionary theory to explain behavior, especially human behavior. E. O. Wilson's (1975) book, *Sociobiology: The New Synthesis*, generated considerable political controversy in the heyday of social relativism, where theories describing the biological bases for behavior were interpreted as a threat to the goal of social equality. More recently, "evolutionary psychology" has emerged as the dominant moniker for the study of evolution and human behavior. The added value that evolutionary psychology brings to the study of evolution and human behavior is the identification of proximal mental processes or mechanisms, which guide behavioral strategies (see Cosmides & Tooby 1994). Darwinian anthropologists and others rightly argue that "evolutionary psychology" may be too narrow as a proper descriptive term. As can be seen in Del Giudice's article, the evolutionary framework crosses traditional disciplinary boundaries and promotes a universally intelligible account that may enhance communication between researchers using quite divergent methodologies.

Tinbergen's (1963) four questions may be used to assess the maturation of explanations for behavior. These questions entail the evolutionary (ultimate) explanations of function (adaptation) and phylogeny (evolution), as well as the proximate explanations of causal mechanisms and ontological development. Del Giudice's overview addresses each of these areas. Del Giudice rightly identifies Darwin's theory of evolution by selection as the only viable account for biological design. He describes how the psychological attachment system is an adaptation to promote reproductive success through the selection of sex-specific reproductive strategies based on the availability of caregivers during development. Biological (including psychological) processes are designed by selection to promote inclusive fitness, and Del Giudice's overview explains why seemingly dysfunctional behavioral patterns are actually useful in promoting an individual's contribution to future generations.

Del Giudice details cross-cultural studies which strongly suggest that the attachment system is a human universal, rather than a product of cultures with particular familiar patterns. In fact, variations in attachment patterns follow the expected direction based on local mating systems and family structures. Del Giudice emphasizes the unique combination of facultative paternal care and cooperative breeding in humans as the key distinction of our species. He notes the existence of adrenal puberty in gorillas and chimpanzees and its absence in other primates and most other mammalian species, as well as the experimental evidence from the manipulation of hormonal levels across a variety of species. However, the phylogenetic context of the attachment system is perhaps the weakest aspect of his overview. This may be easily remedied in part by inclusion of research such as Harry Harlow's maternal-deprivation and social isolation experiments on rhesus monkeys (e.g., Harlow 1964), which were inspired by Bowlby's work on human child institutionalization. A fuller phylogenetic understanding may require further research on species that vary in phylogenetic proximity to humans and on the extent of parental care.

Del Giudice's overview is particularly adept at summarizing proximate explanations. He describes the neuroendocrine bases for the attachment system. Our current understanding of the interplay between psychology and underlying neuroendocrine mechanisms is incomplete, though research is flourishing and likely far from the point of diminishing returns. As models of neuroendocrine systems increase in precision, they will enhance the ability of attachment theorists to specify the causal cascade contributing to patterns of reproductive behaviors.

The theory's depiction of causal mechanisms is properly allied with an account of the developmental processes guiding behavioral strategies. The quality of parental care serves as a proxy for environmental conditions and suggests locally effective strategies. Early caregiving experiences influence attachment styles, which in turn influence reproductive strategies later in life. The LHT emphasis on the importance of the interaction between genes and environment will hopefully further alleviate misconceptions that evolutionary explanations of behavior entail genetic determinism, providing an additional reason to move beyond the unfruitful nature versus nurture debates. The recognition and understanding of adaptive developmental plasticity in Del Giudice's model also provides encouragement and, more importantly, guidance for intervention.

In sum, Del Giudice's account enhances our understanding of the attachment system by integrating findings across several literatures in an evolutionary life history framework. He describes a constellation of phenomena that would be difficult to explain with a competing paradigm or to discount as a "just so" story. His addition of sexual dimorphism in attachment processes proposes further refinement in the description, prediction, and understanding of human psychology and behavior.

Disorganized attachment and reproductive strategies

doi:10.1017/S0140525X0900017X

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Abstract: Del Giudice provides an extension of the life history theory of attachment that incorporates emerging data suggestive of sex differences in avoidant male and preoccupied female attachment patterns emerging in middle childhood. This commentary considers the place of disorganized attachment within this theory and why male children may be more prone to disorganized attachment by drawing on Trivers's parental investment theory.

Del Giudice is to be congratulated for such a bold expansion of attachment theory. The target article resumes the dialogue between evolutionary and developmental theories that proved to be such fertile ground for Bowlby himself. Sex differences in child attachment patterns and their possible preparation for adult mating strategies have been largely neglected within attachment theory, possibly in an attempt to distinguish it from its psychoanalytic origins. Accordingly, a new set of evolutionary hypotheses has emerged that will provide a welcome direction for theoretical integration and future research.

In this commentary, we focus on the integration of disorganized attachment into the life history model, arguing that it may represent a limit to the adaptive function of attachment, and we also aim to briefly draw out some of the clinical consequences of this view. Del Giudice has focused his theory around the organized patterns of attachment while, by his own admission, excluding disorganized attachment. Because the life history theory of attachment is particularly concerned with the reproductive implications of early environmental adversity, disorganization could be considered, especially given that its prevalence is around 15% in low-risk middle-class families (Van IJzendoorn et al. 1999). Furthermore, the prevalence rates tend to increase in proportion to the degree of developmental adversity – parental depression, adolescent parenthood, unresolved loss or trauma and marital discord – reaching a high of up to 80% among maltreating and drug-abusing parents (Green & Goldwyn 2002; Lyons-Ruth & Jacobvitz 1999). Although in some cases a secondary organized attachment pattern can be discerned beyond the disorganized phenomena, at the extreme, cases of multiple attachment strategy in early childhood and unclassifiable adult attachment states of mind (coded as "Cannot Classify" [CC] on the Adult Attachment Interview), suggest a pervasive disorganization of the attachment system that has been found to be strongly associated with child and adult psychopathology (Bakermans-Kranenburg et al. 2005; Green & Goldwyn 2002).

In introducing the formal classification of disoriented/disorganized attachment using the Strange Situation Procedure, Main and Solomon (1990) described its ethological and evolutionary framework as one of "fright without solution" (Hesse & Main 2000). The behavioural indices of disorganized attachment closely resemble phylogenetically conserved mammalian fear responses: flight, attack, and freezing behavior (Main & Solomon 1990). However, in this case, such responses are displayed toward the caregiver who ought to be a haven of safety. Thus, a degree of behavioural conflict occurs between a security-seeking attachment system and a fear-responding survival system. This is reflected in other common indices of disorganization such as simultaneous display of distress and avoidance, undirected or misdirected movements, and disrupted movements or gestures – all of which suggest the enactment of a conflict between approach and avoidance. Such an explanation draws heavily on Bowlby's original assumption that the adaptive function of attachment is largely to do with seeking protection and, therefore, attachment behaviors in infants function to regulate fear via proximity seeking.

Del Giudice cites several studies in which sex differences in the frequency and degree of severity of disorganization have been noted, with male infants tending to be the more frequently and severely disorganized. Males are more prone to aggressive pathology in middle childhood, as has been noted frequently in the conduct disorder literature. An organized response to parental insensitivity in the form of avoidant attachment may well produce an adaptive low-investment parenting strategy for males. However, the more severe modes of aggression associated with disorganization may well produce an antisocial behavioral pattern in males which, like many forms of severe psychopathology, would be maladaptive and reduce reproductive fitness.

Given disorganization's strong association with extremes of developmental adversity and dysregulation of stress responses in infancy and early childhood, why might it be more prevalent in males? Either males are more vulnerable to disorganization, or the primary caregivers of males – typically mothers – are more disorganizing in their caregiving toward male infants under some conditions. In addition to the investigation of proximate mechanisms, there may be an application of the Trivers-Willard hypothesis: namely, for polygynous species, parents in poor conditions are likely to invest more in females, who are more likely to bear them at least some grandchildren, whereas males raised in poor conditions will be unlikely to compete with other males and therefore would attract minimal investment (Trivers & Willard 1973). The evolutionary hypothesis that such fearful and frightening caregiving may be greater toward male offspring would be interesting to investigate.

Evolutionary concepts are increasingly considered in definitions of psychopathology as an impairment of a biologically meaningful function (Wakefield 2005). The pathogenic effect of disorganization may be outside of the average expectable caregiving experiences for which humans are selected. In contrast, avoidant and preoccupied attachments are organized and strategic responses to parental – and most particularly maternal – caregiving, including sensitivity and attunement (see de Wolff & van IJzendoorn 1997). This distinction is an important one because the life history hypothesis serves to reinstate organized but insecure attachments as potentially adaptive in both the social and evolutionary senses, and in the latter, arguably serving to increase reproductive fitness in harsh rearing environments. This suggests that the attachment behavior system is both more robust and flexible than the normative assumptions of ideal security imply. However, beyond a certain threshold, highly adverse caregiving environments involving direct or implied dangers, consistent with maltreatment or caregiver absence (psychological or physical), lead to pathological outcomes and, although it remains to be established, reduced fitness.

Implications for future directions include extensions of the research agenda to psychobiological dysregulation arising from disorganization. Implications of disorganization for pubertal timing and reproductive strategy, mate choice, and degree of parental investment could be investigated. Finally, clarification of the classification of disordered attachment and enhanced clinical interventions can be derived from a better understanding of the biological function and dysfunction of the attachment system across the human life cycle.

Gender difference of insecure attachment: Universal or culture-specific?

doi:10.1017/S0140525X09000181

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Abstract: Our research in China does not show gender differences in insecure attachment patterns. We believe that cultural differences between Chinese and Western societies may help to explain this phenomenon. Mating and parenting circumstances in China do not allow males to adopt a zero-investment strategy. In addition, attachment styles are transmitted across generations and last for the whole lifespan. Here, we argue that the influence of mating and parenting on the well-developed attachment patterns in childhood is relatively small.

In section 6 of the target article, Del Giudice reports a significant gender difference in insecure attachment: Whereas females are more likely to be ambivalent, males are more likely to be avoidant. However, gender differences have rarely been reported in prior studies. We believe that a cross-cultural perspective may help to reconcile this apparent contradiction. In particular, attachment studies in Asian cultural samples, such as China, should be taken into account for a more comprehensive analysis.

Our recent studies in China suggest that there are no gender difference in insecure attachment styles (Li & Du 2005; Li & Kato 2006; Li et al. 2006a; 2006b; 2006c; 2007; 2008; Wan & Li, in press). Table 1 summarizes the results of our relationship questionnaire (RQ) among various samples, including middle school and college students, company employees, and inpatients. Pearson Chi-square tests showed that neither sample had significantly different attachment patterns between males and females. We also note that in the urban mother sample, anxious/ambivalent is most popular among three insecure patterns, with 60.8% secure, 18.5% dismissing, 10.8% preoccupied, and 9.9% fearful (Li 2005).

Del Giudice argues that males and females strive to maximize their reproduction of genes. Gender differences in mating, reproduction, and parenting efforts lead to diverse attachment styles: insecure females tend to be anxious/ambivalent, while insecure males tend to be avoidant (sect. 6.3.1, para. 5). However, reproductive investment alone does not account for the total cost of reproduction and parenting. Females have the privilege of selecting the most suitable male to help with child-rearing (Clutton-Brock 1991). Transitional China, since the 1980s, has been one such example, where parental investment is significantly higher than that in Western nations (Wang & Ollendick 2001). During the 1980s, the Chinese government began to implement a family planning ("one child") policy to control population growth; this policy profoundly changed the demographic as well as cultural values in Chinese society (Arnold & Liu 1986; Xu et al. 2007). First, this policy does not allow males to have multiple children, which requires males to invest in the quality

Table 1 (Li et al.). *Gender-based comparison of attachment patterns from Chinese samples*

Sample	Secure	Dismissing	Preoccupied	Fearful
Middle-school students (Chi-square [3] = 0.717; $P = .869$)				
Male	51	25	21	4
Female	46	21	18	6
College students (Chi-square [3] = 5.901; $P = .117$)				
Males	191	109	109	34
Females	180	93	80	47
Company employees (Chi-square [3] = 4.136; $P = .247$)				
Males	106	61	50	32
Females	107	54	30	33
Inpatients (Chi-square [3] = 3.156; $P = .368$)				
Males	10	12	2	5
Females	8	8	4	1

of offspring, rather than in the quantity (Wang & Ollendick 2001). This greatly reduces the likelihood of males taking a zero-parenting strategy. Second, the traditional preference for sons was even exaggerated, and the "one child" policy often became a "one son" policy, creating an unbalanced gender ratio (Chan et al. 2006). In this case, males have to compete for a limited number of females. Finally, the women's rights movement has been widespread since the communist liberation in the early 1950s, when the socio-economic status of women improved considerably. Recent studies have shown that during family purchase decisions, females now play a status role equal to that of males (Dong & Li 2007). Thus, for contemporary Chinese females, although they cannot shift the balance between parenting and mating effort as easily as men do, they do not need to develop an anxious/ambivalent attachment strategy to invite paternal investment.

A gender difference in insecure attachment could also be explained from the perspective of intergeneration transmission. According to Bowlby (1980), people develop their mental representations of the environment and significant others on the basis of their experience with parents or other caregivers. Bowlby labeled this mental representation as an internal working model (IWM). Once formed, IWMs tend to remain stable for the person's entire lifespan (Hu & Meng 2003). The stability of IWM produces similar attachment patterns from childhood to adulthood. This argument is supported by cross-sectional and longitudinal studies (Brennan et al. 1998; Durrett et al. 1984; Fraley & Spieker 2003; Hu & Meng 2003; Li & Kato 2006; Nakao & Kato 2003). Li (2006) summarized the distribution of attachment styles in infants and adults in Chinese and American samples. He found that the proportion of each attachment style was similar for both infants and adults. This result suggests that the attachment style may remain relatively stable across the lifespan. Longitudinal studies on attachment development also support the stability of attachment styles within generations (Emery et al. 2008; Shemmings 2006). The stability of attachment from infancy to adulthood suggests that the influence of mate selection and sex competition in early adulthood on attachment patterns is trivial. This may well explain the lack of gender difference in insecure attachment in Chinese samples.

In conclusion, we propose that the gender differences of insecure attachment are not universal, but rather, depend on culture input. In China, parenting strategies and intergeneration transmission result in similar attachment patterns between males and females.

ACKNOWLEDGMENTS
This study was supported by the Natural Science Foundation of China (No. 70572007). We thank Mark Sheskin and Adam Pearson for useful comments and suggestions.

The contribution of comparative research to the development and testing of life history models of human attachment and reproductive strategies

doi:10.1017/S0140525X09000193

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Abstract: Research with nonhuman primates can make important contributions to life history models of human attachment and reproductive strategies, such as: including parental responsiveness into female reproductive strategies, testing the assumption that adult attachment is a reproductive adaptation, assessing genetic and environmental effects on attachment and reproduction, and investigating the mechanisms through which early stress results in accelerated reproductive maturation.

Life history theory is a branch of evolutionary biology that deals with the trade-offs in the allocation of time and resources over an organism's lifespan, as Del Giudice discusses in the target article. Concepts and data from animal research played a central role in the development of life history theory. Animal research can also make an important contribution to the development and testing of life history models of human reproductive strategies. In particular, given the similarities in parenting, attachment, lifespan development, and reproduction between humans and other primates (Kappeler & Pereira 2003; Maestripieri 2003; 2005b), studies of nonhuman primates can make a significant contribution to our understanding of human attachment and reproductive strategies.

In rhesus monkeys, infants possess an attachment system whose design features, ontogeny, and adaptive functions are very similar to those of the infant attachment system in humans (Maestripieri 2003; Maestripieri & Roney 2006). These similarities suggest that the attachment system is not a product of the modern human environment, but rather, an adaptation with a phylogenetic history that can be traced back to the common ancestor of humans and Old World monkeys. The infant attachment system in rhesus monkeys is best viewed as an ontogenetic adaptation with the specific function of increasing infant survival during a period of high vulnerability and dependence on a caregiver (Maestripieri & Roney 2006). Attachment theorists have hypothesized that the attachment relationship with a caregiver becomes a template for other relationships later in life, and especially for sexual and romantic relationships. In this view, attachment would be an adaptation not only for early survival, but also for reproduction.

The hypotheses that human adult romantic attachment is an adaptation and that different attachment styles represent different reproductive strategies are currently not supported by strong empirical evidence. These hypotheses, however, could be supported by comparative and phylogenetic evidence showing that attachment serves reproductive functions in closely related primate species, and that humans and these primates are likely to share this reproductive adaptation by virtue of common descent (Maestripieri 2005b; Roney & Maestripieri 2002). Unfortunately, this comparative and phylogenetic evidence is currently lacking. Because the sexual and mating behavior of nonhuman primates appears to be fully accounted for by sexual selection theory (Kappeler & van Schaik 2004), the relationship between attachment and mating has not been investigated in primates. It is, of course, possible that attachment has acquired new reproductive functions in humans, which are not shared with nonhuman primates. As is generally the case with all negative evidence, the failure to find an association between adult attachment and reproduction in nonhuman primates would be difficult to interpret. However, evidence that variation in attachment is associated with variation in reproduction among closely related primates would provide important support for one of the crucial assumptions of the model presented in the target article.

Another assumption of the model is that the timing of menarche is an important expression of female life history strategies in humans, and that variation in the timing of menarche can differentiate between individuals pursuing different reproductive strategies.

Although this assumption is probably correct, research with rhesus monkeys and other primates has suggested that the onset of menstrual activity is only one of a suite of reproduction-related traits associated with different life history strategies. In mammals and birds, variation in offspring survival accounts for the largest fraction of variation in female reproductive success (Clutton-Brock 1988). Accordingly, in rhesus monkeys, the success of a female's first reproductive attempt depends to a large extent on the amount of parenting experience the monkey acquired as a juvenile. Therefore, early menarche and sexual activity are accompanied, and most often also preceded, by early and intense interest in other females' infants (Maestripieri & Roney 2006). Consistent with the predictions of Del Giudice's life history model and its predecessors, research with rhesus monkeys has shown that females exposed to harsh and unpredictable parenting in infancy are more interested in infants early in life than females without this stressful experience (Maestripieri 2005a).

By using cross-fostering experiments, we were able to disentangle the effects of early stress from genetic similarities between mothers and daughters, and by collecting physiological data we were able to show that the effects of early stress on the development of parental responsiveness are mediated by long-term changes in the activity of the hypothalamic-pituitary-adrenal axis (Maestripieri 2005a). Early and intense interest in infants was also observed among adolescent girls who grew up without their fathers at home and had early menarche (Maestripieri et al. 2004). Therefore, parental responsiveness is an important variable that should be included in life history models of human attachment and reproductive strategies. Studies of nonhuman primates can enhance our understanding of different components of human reproductive strategies, both conceptually and empirically.

Lack of control for genetic effects on variation in attachment and reproduction, and lack of knowledge of the physiological mechanisms through which early stress affects reproductive maturation, are some of the limitations of life history models of human attachment and reproductive strategies. Experimental studies of nonhuman primates in which genetic and physiological variables can be manipulated provide opportunities to test some of the assumptions and predictions of models of reproductive strategies in ways that would not be possible in humans. They also provide the opportunity to conduct longitudinal studies of lifespan development and reproduction in a relatively short period of time. Therefore, proponents of human life history models should explicitly encourage the testing of these models with comparative data, and acknowledge that these data can provide important evidence concerning the adaptive function, physiological regulation, ontogeny, and phylogeny of human social and reproductive behavior.

Adaptive developmental plasticity might not contribute much to the adaptiveness of reproductive strategies

doi:10.1017/S0140525X0900020X

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Abstract: Del Giudice's model belongs among those that highlight the role of adaptive developmental plasticity in human reproductive strategies; but at least three other forms of evolutionary adaptation also influence reproductive behavior. Similar to earlier models, the existing evidence suggests that Del Giudice's hypothesized effects are rather weak. In particular, adult attachment styles are hardly predictive of outcomes visible to natural selection.

Del Giudice presents a thoughtful overview, integration, and extension of the now copious literature on what is arguably the most influential developmental hypothesis in modern evolutionary psychology: Children infer environmental risk from cues within their families and adjust their development so that they are well adapted to the reproductive conditions they will face as adults. This is a case of adaptive phenotypic plasticity by conditional development, or adaptive developmental plasticity.

Theoretically, adaptive developmental plasticity is a perfectly plausible form of evolutionary adaptation (Pigullici 2005; West-Eberhardt 2003). However, there are at least three other forms that are equally plausible, and they can all be aligned along a dimension of spatiotemporal environmental stability (Fig. 1).

When fitness-relevant environmental features are stable over tens of thousands of years or longer, organisms can evolve

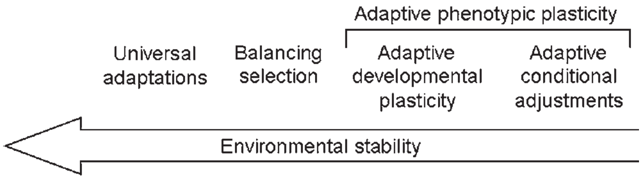

Figure 1 (Penke). Four forms of evolutionary adaptation. They should be understood as distinguishable points along a continuum, not as distinct categories: Balanced genetic variants can get fixated in the population and thus contribute to evolved adaptations, or they can underlie individual differences in either of the two forms of phenotypic plasticity (Belsky 2005; Pigullici 2005), which themselves only differ in how quickly they react to the environment. Which mechanism governs adaptation depends on the spatiotemporal stability of the adaptively relevant environmental features. Different aspects of complex adaptations like life history strategies can be influenced by different mechanisms.

universal adaptations that reliably develop every generation (Tooby & Cosmides 2005). Examples from the domain of human reproductive strategies include the romantic attachment system, which likely evolved in response to the high degree of parental care demanded by human offspring (Fraley et al. 2005), and sex differences in the desire for sexual variety, which are basically adaptive so long as women get pregnant and men do not (Schmitt et al. 2003b).

When the environment is less stable and tends to fluctuate, balancing selection by environmental heterogeneity can maintain more adaptive genetic variants at higher frequencies in the population (Penke et al. 2007b). For example, it has been argued that the phenotypic effects of the seven-repeat allele of the DRD4 polymorphism were more adaptive in societies in which reproductive success is dependent on social competition, whereas the four-repeat allele was likely more advantageous when environmental harshness demanded biparental cooperation (Harpending & Cochran 2002). A similar logic might hold for the heritable components of traits related to reproductive strategies (e.g. Schaller & Murray 2008), including the polymorphisms affecting children's sensitivity to rearing environments in Del Giudice's model (Belsky 2005). However, it will likely not hold for the genetic foundations of the "K-factor," which is far less plausible from an evolutionary genetic perspective (Penke et al. 2007a; 2007b).

Even less stable and more heterogeneous environments favor the evolution of adaptive phenotypic plasticity (Hollander 2008), which includes developmental plasticity, as discussed by Del Giudice, and much faster adaptive conditional adjustments of life history strategies to the current environment. Examples of the latter include adjustments of strategic mating decisions to momentarily faced environmental harshness, quality of available mates, or sex ratio and competition on the local mating market (Gangestad & Simpson 2000; Penke et al. 2007c; Lenton et al., in press). Importantly, romantic attachment styles also show considerable plasticity during adulthood and might even be relationship-specific (Lehnart & Neyer 2006).

These four different forms of adaptation are not mutually exclusive. I agree with Del Giudice that they will likely all contribute to individual differences in reproductive strategies in a probabilistic manner. However, the critical – and ultimately empirical – question is their relative importance. And this is where I find adaptive developmental plasticity hypotheses of reproductive strategies problematic. When the earlier models that predicted pathways from childhood stress to age of menarche in girls to adult reproductive strategy were empirically tested, hardly any evidence could be found (Ellis 2004; Hoier 2003; Neberich et al., in press). These results led some researchers to retract reproductive strategies altogether and to concentrate on the stress–menarche link (Ellis 2004).

Del Giudice's model, on the other hand, attempts to rescue the causal relationship between childhood stress and adult reproductive strategy by relying much more on attachment styles as the mediating factor and introducing some elegant theoretical refinements, including sex differences and children's attachment styles as disposable phenotypes. However, although there is abundant evidence that adult attachment styles relate to the construal and experience of romantic relationships (Birnbaum et al. 2006; Feeney 1999), there seems to be surprisingly little evidence that romantic attachment styles actually relate to reproductive strategy-related consequential behavioral outcomes. This is a crucial point, because only consequential behaviors, not subjective experiences, are visible to natural selection and can thus be reasonably explained within an evolutionary framework.

To give an example, sociosexuality shows almost no relationship with attachment styles (Schmitt 2005a). Strikingly, only restricted sociosexual attitudes, but not sociosexual behaviors, were related to attachment styles in a study by Jackson and Kirkpatrick (2007), but Penke and Asendorpf (in press) showed that attitudes were the only component of sociosexuality not related to a variety of behavioral outcomes, much like self-reported mate preferences are unrelated to actual mate choices (Todd et al. 2007). As another example, attachment styles are not predictive of romantic relationship stability once relationship duration is taken into account (Lehnart & Neyer 2006), and avoidant men and anxious women can have as stable relationships as securely attached people, no matter how satisfied they are with it (Kirkpatrick & Davis 1994). Even the sex differences in insecure adult attachment styles, which enjoy a prominent role in Del Giudice's model, are in fact quite modest in size (Schmitt 2005a; Schmitt et al. 2003a, being much smaller than in other mating-related dispositions (e.g., Schmitt 2005b; Schmitt et al. 2003b). Indeed, it could be argued that their size, even in harsher environments, is too small to be theoretically meaningful (Hyde 2005).

To conclude, although the available evidence is clearly insufficient to fully evaluate Del Giudice's complex model, it suggests that adaptive developmental plasticity might not account for much variance in reproductive strategies. The theoretical reason for this could be straightforward: During human evolution, environmental changes in reproductive conditions over a few generations were probably less important for successful propagation than changes over much longer or shorter time spans, which lead to universal adaptations, polymorphisms under balancing selection, and adaptive conditional adjustments related to reproductive strategies. Still, I am confident that the myriad of intriguing ideas in Del Giudice's article will inspire future studies, which will hopefully confirm how big or small the contribution of adaptive developmental plasticity to reproductive strategies really is.

ACKNOWLEDGMENTS

The author is funded by the UK Medical Research Council. The UK Medical Research Council and the University of Edinburgh provide core funding for the MRC Centre for Cognitive Ageing and Cognitive Epidemiology, which supported this research. Thanks to Jaap Denissen and Michelle Luciano for helpful comments.

Modeling, simulating, and simplifying links between stress, attachment, and reproduction

doi:10.1017/S0140525X09000211

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Abstract: John Bowlby's use of evolutionary theory as a cornerstone of his attachment theory was innovative in its day and remains useful. Del Giudice's target article extends Belsky et al.'s and Chisholm's efforts to integrate attachment theory with more current thinking about evolution, ecology, and neuroscience. His analysis would be strengthened by (1) using computer simulation to clarify and simulate the effects of early environmental stress, (2) incorporating information about non-stress related sources of individual differences, (3) considering the possibility of adaptive behavior without specific evolutionary adaptations, and (4) considering whether the attachment construct is critical to his analysis.

One of the key innovations in Bowlby's attachment theory was to replace Freud's drive theory with a motivational model based on control systems theory. Concerned that this might seem like replacing one bit of magic with another, Bowlby turned to evolutionary theory to explain how an infant could be endowed with an attachment control system. Citing many examples, he argued that evolution shapes not only physical structures but also species learning abilities. Attachment is not an instinct or a preprogrammed blueprint ready to be activated by critical experiences; it is the capacity to construct a behavioral system through the interaction of species-specific learning abilities with information available in the organization of what Bowlby called an average expectable caregiving environment. This was an innovative solution to a difficult problem and continues to serve well despite the fact that Bowlby's emphasis on the value of attachment behavior as an adaptation to predation pressure today seems more "classical" than modern (Waters 2002).

1. Modeling stress and adaptation. Early exposure to environmental stress is central to Del Giudice's analysis. Yet he says little about what constitutes relevant stress and, more importantly, how its characteristics over time might bear on the costs and benefits of different reproductive strategies and patterns of parental investment. Simply put, the effectiveness of behavioral strategies depends on context. Imagine a behavioral ecologist examining avian foraging strategies without considering the implications of foraging for food that is plentiful or spare, concentrated or dispersed, consistently or intermittently available, and so on. In the case of early experience, attachment, and reproduction, it seems likely that the costs and benefits of any particular strategy would depend very much on the incidence, persistence, duration, mortality risk, and other parameters of the environmental stress, as well as on key features of a species' life history strategy. Formalizing the properties of a stressful environment as computational models and using simulation to investigate the costs and benefits of different mating and parental strategies through a wide range of such parameters would enrich Del Giudice's analysis, exploring the robustness of his hypotheses and predictions and possibly highlighting some interesting circumstances that deserve special attention. There are a number of existing approaches that might be adapted for this purpose; for example, simulations concerned with the evolution of protection periods (Bullinaria 2007), the growth of social complexity (Doran 1994), and simulation of secure-base behavior (Petters 2006a).

2. Attachment patterns without stress. In light of Del Giudice's emphasis on the role of stress in shaping attachment patterns, it is useful to consider that individual differences can arise without stark ecological stressors. A dismissing or preoccupied adult or an avoidant or resistant baby is not necessarily one whose experience has been pathological. Temperament, garden-variety diversity in caregiving experiences, and idiosyncratic interpretations of personal experience guarantee, even in benign environments, a rich diversity of attachment patterns within individuals and across time. This point is underlined in computational experiments (e.g., Petters 2006b) in which distinct attachment styles can arise merely from the action of positive feedback loops acting upon small, random differences in the environment. Del Giudice's analysis would be considerably strengthened if it were expanded to address conceptually and in terms of physiological mechanisms, how, in light of these non-stress related sources of individual differences, the attachment system's sensitivity to stress could be tuned so it is neither insensitive to significant stressors nor overly responsive to minor perturbations.

3. The adaptationist fallacy. In Del Giudice's analysis, the effects of early environmental stress on attachment include effects on attachment-related physiology. These are interesting and testable hypotheses. However, it is worth keeping in mind that adaptive behavior does not always imply an underlying "adaptation." As Bowlby (1969/1982) argued, attachment relations can be represented at a variety of levels, from the organization of underlying physiological systems, to reactive fixed action patterns, to mental representations (internal working models) and natural language (Bowlby 1969/1982). Accordingly, adaptive behavior might also be explained by cognitive processes – allowing early experience to shape mental representations and social perception in ways that impact adaptively on courtship, mating, and parenting. Nor are these two routes to decision making independent or mutually exclusive. Designing computer simulations that integrate lower-level reactive mechanisms with simple reasoning processes (e.g., Petters 2006a, Ch. 4) seems a promising approach to exploring the roles of evolved adaptations and rational adaptive behavior.

4. Is attachment critical to the argument? As Del Giudice notes, there are two distinct traditions in attachment assessment: one based on infant observation and adult interviews, and the other based on adult self-report questionnaires. Both traditions are inspired by Bowlby's theoretical work, and both use similar terminology to describe the constructs they measure, describing individuals as secure versus anxious or insecure, and as anxious, avoidant, ambivalent, and so on. Both approaches have produced useful empirical results. However, measures from the two traditions do not yield correlated scores and have rather different patterns of stability and change, different behavioral correlates, and different relevance to courtship, marriage, and parenting (Waters et al. 2002). Although acknowledging some of the difficulties here, Del Giudice tends to treat similarly named measures as if they were interchangeable. This is too much to expect readers to track and undermines the conceptual and empirical foundations of key elements in his analysis. In addition, the correlations underlying links between types of insecure attachment and traits, such as aggressive/self-aggrandizing or fearful, passive, withdrawing, and so on, are typically very small or inflated by considerable method variance. Such low correlations, and the fact that they represent data from different measures and different age groups, substantially attenuate the empirical link between attachment and the patterns of mating and parental behavior at the heart of Del Giudice's analysis. We wonder whether the link between early stress and later reproductive behavior might be better argued by having early experience directly affect approach and avoidance systems – without mediation through attachment.

5. Conclusion. Del Giudice's analysis of links between early stressful environments, attachment, and reproduction illustrates some of the advantages – and some of the difficulties – of coordinating current attachment theory with current ideas about evolution, ecology, and life history strategies. There is no doubt that John Bowlby would have appreciated such efforts and looked forward, as we do, to further advances along these lines.

Predicting cross-cultural patterns in sex-biased parental investment and attachment

doi:10.1017/S0140525X09000223

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Abstract: If parenting behavior influences attachment, then parental investment (PI) theory can predict sex differences and distributions of attachment styles across cultures. Trivers-Willard, local resource competition, and local resource enhancement models make distinct predictions for sex-biased parental responsiveness relevant to attachment. Parental investment and attachment probably vary across cultures in relation to "local fitness currencies" for status, wealth, and well-being.

Attachment may play a crucial role in the development of human mating and parenting behaviors. Hence, the evolutionary design of attachment could be revealed in relations among risk, resources, and parenting. Del Giudice presents a welcomed and state-of-the-art synthesis of attachment research in evolutionary context. The task ahead is to explore empirical avenues to test and refine predictive models. Data and hypotheses concerning associations between attachment and environmental conditions across populations are particularly scarce, suggesting a fruitful area for future research. Del Giudice's analysis of sex differences in attachment suggests some intriguing questions: What environmental conditions promote boys' and girls' attachment styles, either to diverge into more pronounced patterns of avoidance and anxiety in some populations, or to converge, creating higher proportions of secure individuals in other populations? Is it possible for one sex to show a high proportion of security while the other sex experiences greater insecurity? Do environmental effects on attachment shape patterns of cultural diversity in reproductive behavior? Addressing these questions could enhance our understanding of attachment and its role in larger cultural patterns related to mating, parenting, family, and risk. Here, I focus on sex-biased parental investment and predicted associations with reproductive and family behaviors cross-culturally.

Sex-biased parental care may be expressed as differential parental responsiveness to boys and girls, which could promote divergent attachment styles for males and females. Parental investment theory offers standard models for sex-biased investment (Clutton Brock 1991). Trivers and Willard's (1973) model describes several conditions: (1) one sex has higher variance in reproductive success than the other; (2) offspring's reproductive success is sensitive to the parental care they received; and (3) parental care is positively correlated with parental condition. Under these assumptions, parents in good condition could maximize long-term fitness by biasing their attention toward children of the sex with higher reproductive variance. Conversely, parents in poorer condition should bias attention toward the sex with less reproductive variance. Patterns of parental investment fit this model in some human populations (Cronk 2000). Under Trivers-Willard conditions, we expect to see more secure males and insecure females among relatively wealthy families, and more secure females and insecure males among relatively poor families. The population or culture-level implications of this attachment pattern are intriguing. For example, marriage patterns between the high-status Masai and low-status Mukogodo of Kenya include hypergamy, where Mukogodo families encourage daughters to marry into neighboring, higher-status Masai families. This marriage preference creates a problem for Mukugodo men, who sometimes have trouble finding mates; hence, Mukugodo parents tend to bias investment toward daughters. Daughter bias is evident early in infancy, when daughters are more likely to be seen suckling and being held than are sons (Cronk 2000). This is precisely the kind of sex bias in child care that could enhance divergences in attachment style.

Trivers-Willard fails to predict parental investment in many human and other primate populations, probably because additional factors can affect sex-specific returns on parental investment. Local competition among same-sex siblings is a common complication that can weaken the Trivers-Willard effect. If one sex competes for parental resources, then competition can create lower offspring fitness returns per unit of parental investment. Local competition among brothers is not uncommon cross-culturally (Borgerhoff Mulder 1998; Quinlan et al. 2005), and it may promote female-biased investment, leading to higher levels of security among girls. Local competition can be quite strong in polygynous societies, in which brothers compete for access to parental resources crucial for accruing multiple wives. In that case, we expect relatively high levels of avoidance among males and higher levels of secure attachment among females.

Note that local mate competition in polygynous societies is probably associated with high variance in male reproductive success – a key element in the Trivers-Willard effect – which can create a series of rather complex parental investment decisions. For example, among the agro-pastoralist Kipsigis of Kenya, polygyny, livestock payments made for brides, and patterns of sibling interaction create a mosaic of parental investment considerations that fit multiple models of parental investment (PI) (Borgerhoff Mulder 1998). Predicting attachment patterns among groups like the Kipsigis will require close attention to underlying parental investment concerns related to "local fitness currencies"– local resources and relationships that are associated with cultural and reproductive success.

A third pattern of sex-biased parental investment may present additional challenges for evolutionary theories of attachment. Local resource enhancement occurs when offspring of one sex help care for siblings or other relatives, which reduces the costs of parental effort. Parents tend to bias investment toward helpers because a portion of that investment is repaid through work that can enhance parental fitness. In that case, helpers can receive more direct parental care than non-helpers (Quinlan et al. 2005). This empirical pattern is at odds with the proposed attachment style promoting helping at the nest: Helpers are predicted to have insecure clingy styles (Chisholm 1996); yet biased parental care under local resource enhancement suggest that helpers could be securely attached in many circumstances. The role of anxious attachment style (if any) in promoting helping-at-the-nest requires verification in societies with substantial cooperative childrearing at the household level, which is common cross-culturally but relatively rare in many Western industrial populations.

Sex-specific risks (and saturation points for parental effort) can further complicate parental investment decisions. In some populations, one sex can face greater extrinsic risk than the other. For example, in rural Dominica, boys and men consistently experience greater fitness risks and fewer opportunities than girls and women do. Asymmetry in risk may promote daughter-biased parental investment that includes later weaning (by 5 months in Dominica), greater direct parental care during childhood, and more investment in education in adolescence (Quinlan 2006). Attention to sex-specific risks will probably prove instructive in the years to come.

Not all parental investment occurs during the sensitive period for attachment. Some parental resources may affect fitness, but they can have little impact on attachment. Family wealth could be channeled toward sons or daughters independent of parental responsiveness in early childhood. Parents in Germany, for example, invest substantial wealth in offspring, but parental care in infancy and early childhood promotes independence and a degree of physical and psychological distance that may seem distressing when viewed from other cultural models of parenting (Levine & Norman 2001).

In sum, patterns of investment and their likely influence on attachment depend on local fitness "currencies" based on prevailing or anticipated economic, ecological, and social factors. Accurately predicting the distribution of attachment styles in and across populations will probably require close attention to multiple local dimensions of parental investment.

Neuroendocrine features of attachment in infants and nonhuman primates

doi:10.1017/S0140525X09000235

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Abstract: The translation of research findings from other primates to humans, and from infants to adults within our own species, requires great care. If the many neurological, behavioral and adaptive distinctions between these groups are not precisely defined and considered, erroneous conclusions about evolutionary history and developmental processes may result.

Research on primates reveals the myriad ways in which animals can alter their behavior to accommodate environmental change. Del Giudice's argument that human sexual behavior may also be facultative represents a significant contribution to this larger literature, with important implications for both human evolutionary biology and developmental psychology. We applaud this effort to unite these fields; indeed, it is likely that many aspects of human emotional behavior are important targets for natural selection.

Extrapolation of findings across age groups or species, however, is rarely straightforward, and the argument articulated by Del Giudice would be strengthened by greater sensitivity to the inherent limitations and challenges of such an enterprise. We illustrate this point in two ways. First, we underscore the need for precision when drawing analogies between humans and other primates by discussing how adaptive physiological mechanisms in other taxa may not act correspondingly in our own species. Second, we advocate caution when attempting to map specific biological systems onto relatively unspecified behaviors or feeling states. Emotions, such as those that mediate relationships in adult humans, are often difficult to assign clearly into those that are (or were) adaptive and those that are (or were) not.

An example of our first point is highlighted by Del Giudice's suggestion that human females practice facultative reproductive suppression by developing a lack of interest in sexual relationships when the social support systems necessary to help with childrearing are absent. While it is probable that humans are cooperative breeders, reproductive suppression in the context of cooperative breeding in other primates is accompanied by specific physiological, behavioral, and neuroendocrine mechanisms that have no parallel in humans. The best-known data concerning this phenomenon come from the marmosets and tamarins of the New World, who appear to utilize reproductive suppression in the context of kin selection (Hamilton 1964). Subordinate individuals in these species assist in the rearing of the offspring of a much smaller number of related dominants, who are typically the only ones who become pregnant (Carlson et al. 1997). This is caused by a pheromonal–behavioral mechanism that regulates the process whereby dominant females prevent subordinate females living in the same group from ovulating (Barrett et al. 1990). In fact, prevention of ovulation is the most widely used definition of reproductive suppression, with clear physiological correlates. For example, the ovaries of dominant females are 50% greater in volume than those of subordinates and have many more antral follicles, whereas subordinates lack corpus lutea and do not release sufficient lutenizing hormone for ovulation to occur (Abbott et al. 1998). When a subordinate female is removed from her natal social group, however, this constraint is released, which can lead to pregnancy as few as eight days later (Ziegler et al. 1987). In other words, it is the very presence of related females who could provide rearing support that causes reproductive suppression, not their absence. This is opposite to the scenario envisioned by Del Giudice. Although the term "reproductive suppression" does have other applications in the biological sciences, it is misleading to use this term to refer to mating avoidance in healthy females who are otherwise capable of reproducing successfully. In this case, Del Giudice's argument suggests a parallel between primate physiology and human behavior that is incorrect: There is no evidence indicating that such a phenomenon occurs in human females.

Our second and related point is that it is difficult to map clear, well-defined physiological mechanisms onto general behavioral constructs in humans. Del Giudice demonstrates creativity and thoughtfulness in attempting to link neurophysiology and evolution to a construct such as "attachment." As he defines "attachment," however (and indeed, how most psychologists now use the term), it is unlikely to be tied to any clear biological circuitry. We agree that discontinuity between infant and adult attachment is likely even though some of the same neural and endocrine systems, such as oxytocin-mediated social bonding, are involved. The author makes this point as well, suggesting that adrenarche represents a hormonal disconnect of behaviors advantageous in infancy from those that may be advantageous in adulthood. What is lacking is a precise, neurologically plausible definition as to what attachment means in human adults, as well as reliable tools for measuring it.

In infancy, attachment is characterized by a cessation of exploration, initiation of proximity to the caregiver, or distress if the caregiver is unavailable. The same behaviors are apparent in other primate infants as well, suggesting that intra-species comparisons of attachment may be justified in this specific case. In chimpanzees, for example, the mature caregiver provides a secure base from which the infant can explore and seek comfort, and one can interpret changes in hypothalamic-pituitary-adrenal axis activity as an index of the caregiver's effectiveness in reducing infant stress (Miller et al. 1986). In human adults, however, attachment is construed broadly as a personality variable that is not amenable to intercross-species comparisons analyses. For example, adult attachment is often operationalized as the coherence of narrative responses to questionnaires or interviews. Such information is undoubtedly a rich source of data, but this type of data taps into cultural expectations, is difficult to relate to the behavioral and physiological phenomena observed in human and nonhuman infants, and is not directly related to the social behaviors observed in other species. For these reasons, it is difficult to reach firm conclusions about the evolutionary significance of attachment as it is construed in human adults.

We admire Del Giudice's thesis as a noteworthy effort toward a better understanding of the evolutionary underpinnings of modern human adult relationships. Empirical studies of human biobehavioral plasticity, and the adaptive advantages such plasticity may confer, require thoughtful integration across species and across the ontogenetic spectrum, with special attention paid to the role of species-typical and species-atypical contexts. When done appropriately, such research is likely to excavate the biobehavioral processes that promote social competencies and health.

Attachment styles within sexual relationships are strategic

doi:10.1017/S0140525X09000247

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Abstract: Del Giudice's examination of sex differences in reproductive strategy within an attachment context is well taken. Sex has been studied as behavior within romantic relationships, but attachment styles should also be reflected in strategic behavior within relationships that are sexual. This seems particularly true within adolescence, and sex differences may be better reflected as differences in correlation patterns of process variables than as main effects models.

Attachment theory (e.g., Bowlby 1969/1982) has been used so widely in research and practice that it is easy to forget its theoretical roots in control systems, ethology, and the development of behavior within an evolutionary context. Del Giudice correctly directs attention on a neglected component of this theory: human reproductive strategies. Although attachment, caregiving, and sex have historically been argued to be three independent systems (e.g., Ainsworth 1989), this suggestion seems based on comparative data on the behavioral manifestations of mate attraction and the sexual response. Sex is a behavior that happens within romantic relationships; for example, Davis et al. (2004) portray sex as a behavior that serves attachment needs (see also

Butzer & Campbell 2008). But the evolutionary context of relationships involves a combination of these three systems (see Mikulincer 2006), and Del Giudice's proposal that sex differences in attachment have adaptive significance places an emphasis on this very issue. That is, attachment processes are an essential component and are thus reflected in sexual relationships, which follows on the respective work of Belsky (2007; Belsky et al. 1991) and others (e.g., Brumbaugh & Fraley 2006; Chisholm 1999).

Del Giudice encourages an essential expansion of the evolutionary elements of attachment because adaptive significance includes infant survival, sexual relationships, and, then, parenting commitment to the young in the next generation. In general, attachment research has focused primarily on the first and last of these three components; but what Del Giudice refers to as the "double life" of the attachment system through care-eliciting and pair-bonding needs to expand on the reproductive strategy component. This should be particularly true in adolescence, when sex is a dominant focus of attention, teens typically have a series of sexual partners, and risky sexual behavior poses health risks that have immediate and long-term consequences for reproductive life history strategies. Three points are made in this commentary: (1) that sexual behavior needs to be examined within the attachment context of sexual relationships; (2) that this seems particularly true within adolescence, when sex is a dominant theme and goal; and (3) that sex differences need to be examined as differences in correlation patterns in addition to main effects models.

Research on adult romantic attachment addresses intimacy, dependency, and trust issues within "emotionally intimate relationships" (Bartholomew & Horowitz 1991; Hazan & Shaver 1987; for review, see Hazan et al. 2006), which is related to some aspects of sexual behavior (see Brennan et al. 1998; Davis et al. 2004; Milkulincer & Goodman 2006). However, romantic attachment is not necessarily synonymous with sexual relationships. While romantic relationships usually contain a sexual element, not all sexual relationships are romantic ones (e.g., sex between friends, one-night stands), nor are all romantic relationships perceived as such after they have ended. Attachment insecurity may manifest itself in promiscuity, using sex to maintain a relationship, sexual coercion, and separation of sex from emotional caring for a partner, but these are domain-specific behaviors and motivations within sexual relationships (reviewed in Feeney & Noller 2004). As noted by Belsky (2007), these vary from opportunistic advantage-taking approaches to sex (i.e., avoidant) to dependent helper-at-nest kinds of approaches (e.g., ambivalent/ preoccupied). When attachment-relevant self-report items focus on behavior with sexual partners, there is the potential to predict strategic sexual behavior above and beyond that predicted by romantic relationships (see Szielasko et al. 2007; under review).

This distinction between sexual and romantic partners may be particularly relevant to teens who are very interested in sex, typically have a series of sexual partners during adolescence and early adulthood, and may be more motivated by physical attraction than an evaluation of partners in terms of future co-parenting investment. Del Giudice frames this issue within life history theory when he distinguishes between mating effort and parenting effort, wherein teens are usually invested in the former and not the latter. Downward extensions of adult-oriented attachment measures (e.g., Allen & Land 1999; O'Connor & Byrne 2007) may mask the significance that sexual behavior and misbehavior have with regard to later relationships and developmental processes for late teens (see Feeney et al. 1993; Kobak et al. 2007). Keep in mind that human evolution took place over a time frame when pregnancy was not controllable, so adolescence is the developmental period when pregnancies historically arose, not adulthood, when current-day pregnancies are often fit in with other life history strategies of investment.

Del Giudice addresses sex differences in attachment, but most of the literature reviewed uses a main effects model of sex that describes avoidant males and ambivalent/dependent females (i.e., investment-eliciting). Although these patterns fit his theory, no doubt there are avoidant females and preoccupied males whose sexual adaptations must also be considered. If ambivalence is related to sexual coercion and avoidance related to promiscuity (see Bartholomew & Allison 2006; Feeney & Noller, 2004; Szielasko et al. 2007), for example, it would be important to know whether this is equally true for both males and females, and how coercive behavior may vary between the sexes when a relationship feels threatened (e.g., physical force? trickery?). Such a finding would not necessarily pose a problem for the proposed theory, as ultimately attachment styles reflect adaptations to environmental circumstances, but we argue for a need to address potentially different patterns of correlations between attachment constructs and sexual behavior/misbehavior in males and females.

Del Giudice hints at this when discussing different implications of insecurity for the reproductive strategies of men and women, but he could go even further with this thinking. Literature suggests that avoidance is related to a greater number of less committed sexual relationships, and ambivalence is related to dependency and possessiveness, but is this equally true for both genders, or are there sex-specific manifestations of sexual behavior that reflect these attachment styles? And may these behaviors have different longitudinal consequences for personality development and attachment styles?

Bowlby (1969/1982) wrote that it may be that "attachment and sexual behavior share certain components and causal mechanisms" (p. 233), and considering the adaptive significance of both within the context of adult relationships is essential. This article by Del Giudice promises to invigorate thinking on this component of attachment theory in an evolutionary context, building on the inspiration of Belsky et al. (1991) that took place almost two decades ago.

Attachment and sexual strategies

doi:10.1017/S0140525X09000259

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Abstract: Sexual behaviour and mate choice are key intervening variables between attachment and life histories. We propose a set of predictions relating attachment, reproductive strategies, and mate choice criteria.

Del Giudice presents a meaningful extension of evolutionary models of attachment. The target article builds on existing theory to account for the adaptive consequences of various attachment strategies beyond early childhood relationships with caregivers. The central tenet of this body of theory is that attachment functions as a mechanism for adaptively adjusting human life histories and reproductive strategies to the socio-ecological environment in which children grow up. Del Giudice's major contribution is to focus the issue of sex differences in attachment processes through the lens of sexual selection theory. This provides a cogent interpretation of the different relationships between attachment processes and behavioural and life history outcomes in males and females. It also brings into sharper relief the relatively neglected but vital socio-developmental processes occurring in middle childhood. These are theoretical steps forward, and ones that are consistent with the data reviewed by Del Giudice. The major challenge now is to develop and test a range of more critical empirical predictions.

We propose one particular set of predictions for future research. The hypothesized link between attachment and adaptive variation in reproductive strategies (e.g., mating vs. parenting effort) implies that sexual relationships should be a key area for study. Much evidence suggests that women's sexual strategies correlate with mate preferences on certain dimensions of physical attractiveness, such as male facial and vocal masculinity (Gangestad & Simpson 2000; Gangestad & Thornhill 2008; Provost et al. 2008). In combination with the arguments of the target article, this leads to the prediction that attachment styles should correlate with females' preference for masculine faces and voices. In populations characterized by low paternal investment and high levels of aggressive male–male competition, there is a significantly stronger average preference among females for masculinized facial features than in populations characterized by higher paternal investment (Penton-Voak et al. 2004). The evolutionary logic is that, where there is low paternal investment, women's mate choices should be more strongly biased towards males of high competitive ability. Similarly, women seeking short-term sexual relationships have a stronger preference for masculine features than those seeking long-term relationships (Little et al. 2002), again indicating a link between likelihood of paternal investment and preference for masculinity. The theoretical link to attachment processes is that female dismissiveness should correlate positively with masculinity preferences. On the other side of the coin, males with more masculine faces tend to have more sexual partners and be less interested in long-term relationships (Boothroyd et al. 2008). Consequently, facial masculinity should correlate with attachment profiles in males.

Sexual strategies also vary according to the individual's perception of their own "market value" (Little & Mannion 2006). An intriguing corollary of the target article is that these perceptions may correlate not only with physical attractiveness, but also with the experience of attachment relationships in middle childhood. This would predict an association between attachment profile and self-rated attractiveness.

Finally, female sexual strategies have been shown to be hormonally influenced. During the menstrual cycle, women become more interested in short-term relationships, are more likely to be unfaithful to their long-term partner, and are more attracted to masculine facial and vocal features around the time of ovulation, when the risk of conception is high (Penton-Voak et al. 1999; Feinberg et al. 2006; Gangestad & Thornhill 2008). This has been interpreted as reflecting a "dual" sexual strategy, promoting mating with competitive but low-investing males while also garnering paternal investment via a long-term relationship. A further prediction is therefore that attachment profiles should vary cyclically, directly mirroring the cyclicity in sexual behaviour. This would imply that attachment profiles, albeit perhaps largely fixed early in life, also have some previously unsuspected adaptive plasticity.

What love has to do with it: An attachment perspective on pair bonding and sexual behavior

doi:10.1017/S0140525X09000260

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Abstract: Del Giudice proposes that short-term mating strategies are adaptive for attachment-avoidant men. We argue that this model (1) does not apply to the majority of avoidant men (fearful-avoidants); (2) is based on limited evidence that the remaining subset of avoidant men (dismissing-avoidants) engage in short-term mating strategies; and (3) disregards the importance of pair bonding even for dismissing-avoidants.

A central assumption of Del Giudice's model is that insecurely attached male infants develop an avoidant attachment strategy in adulthood that is associated with short-term mating strategies that maximize fitness. In this commentary, we first argue that Del Giudice's model ignores the majority of men who engage in avoidant attachment strategies, namely, fearful-avoidant men, who constitute approximately 21% of the population (Bartholomew & Horowitz 1991). Moreover, the model does not accurately apply to dismissing-avoidant men, who make up approximately 18% of the population. Second, we question Del Giudice's claim that the "link between avoidance and short-term mating style is well supported by research in adult attachment" (sect. 5.2, para. 3), as well as the idea that short-term strategies increase fitness for dismissing-avoidant men. Finally, we discuss a point overlooked by Del Giudice: the benefits of pair bonding on, and in the absence of, direct reproductive outcomes.

Del Giudice claims that an avoidant attachment strategy is related to short-term mating strategies (e.g., an earlier onset of first sexual experience and higher frequency of sexual activity with different partners). However, empirical work does not unequivocally support this claim. There is evidence that avoidant male adolescents are less likely to ever have had sex, to have engaged in fewer sexual behaviors before trying intercourse, and to have sex less frequently (Tracy et al. 2003). In a sample of 327 adult men between the ages of 19 and 35 years, attachment avoidance was unrelated to frequency of sexual intercourse (Bogaert & Sadava 2002). Even though there is some evidence that attachment avoidance is associated with a higher frequency of casual sex (i.e., sex in the absence of a committed relationship) (Brennan & Shaver 1995; Schachner & Shaver 2002), this is only true for a subset of avoidant males.

One explanation for this discrepancy is a distinction that Del Giudice relatively ignores: the difference between *dismissing*-avoidance and *fearful*-avoidance. According to adult attachment theory (Bartholomew & Horowitz 1991; Hazan & Shaver 1987), both dismissing-avoidant and fearful-avoidant people are uncomfortable with closeness and intimacy and avoid relying on attachment figures. A critical distinction between the two is in their level of attachment anxiety (i.e., concerns about rejection and abandonment by partners). Dismissing individuals avoid intimacy and closeness because, at least explicitly as part of an emotion-regulation strategy (Fraley & Shaver 1997), they devalue the importance of close others and emotional ties. In contrast, fearful individuals avoid intimacy and closeness because they strongly fear being rejected. Thus, dismissing-avoidance is characterized by high avoidance and low anxiety, whereas fearful-avoidance is characterized by high avoidance and high anxiety.

With respect to sexual behaviors, these two avoidant patterns share some similarities but also differ in important ways. Because both are uncomfortable with closeness, sexual activity is less satisfying, less pleasurable, and even aversive (Birnbaum et al. 2006), and consequently, is engaged in less frequently (e.g., Brassard et al. 2007). However, only dismissing-avoidance is associated with engaging in casual sex in lieu of intimate relationships (Schachner & Shaver 2004).

Thus, Del Giudice's model does not apply to a significant proportion of avoidant individuals, namely, fearful-avoidants. Further, even if one distinguishes between the two avoidant patterns, as proposed by attachment theory, Del Giudice's model may still not be correct with respect to the short-term mating strategies of dismissing-avoidants. Although they engage in casual sex, there is no clear evidence that dismissing-avoidants have an earlier onset of sexual activity (Bogaert & Sadava

2002), or that they engage in other short-term mating strategies, such as extra-paired sexual affairs (Bogaert & Sadava 2002; Gangestad & Thornhill 1997). Thus, there is limited evidence supporting Del Giudice's claim that dismissing-avoidant men engage in short-term mating strategies.

As an alternative explanation, we propose that dismissing men who engage in casual sex do so to satisfy attachment-related needs, irrespective of direct reproductive outcomes. Research shows that avoidant individuals are more likely to cite external motivations for engaging in sex ("to fit in better," "to be able to say you've done it"), which suggests that they engage in sex to seek social status and to avoid peer rejection (Schachner & Shaver 2004). Consistent with the idea that attachment-related needs underlie engaging in sexual behaviors for avoidant individuals, greater frequency of casual sex appears to be independent of sex drive (Schachner & Shaver 2002).

Moreover, we question whether a short-term strategy is more beneficial than a long-term strategy for dismissing individuals. We consider this from both a sexual strategies perspective, in which individuals aim to maximize their fitness, as well as an attachment perspective (Bowlby 1982), according to which individuals aim to maintain close ties with others to promote feelings of security and well being.

From a sexual strategies perspective, pair bonding in humans increases fitness (Hazan & Diamond 2000). It promotes parental investment in offspring, thereby increasing offspring survival. Further, it increases the chance of fertilization, given the covert ovulation cycle in women and that the frequency of women's ovulation cycles increases within pair bonds (Veith et al. 1983). As a result, sex within a committed relationship is more likely to lead to reproductive success than promiscuous sex. Moreover, although individuals who engage in casual sex may have a greater number of partners per year, the frequency of engaging in sex is likely to still be higher for dismissing individuals within committed relationships. In short, it has not been established that a short-term mating strategy will increase fitness for dismissing men.

From an attachment perspective, the physical, psychological, and social benefits of mother–child bonds (Harlow & Harlow 1965) and pair bonds (Uchino et al. 1996) are well-documented. The magnitude of attachment-related benefits on health and mortality are approximately the same as the detrimental effect of smoking on health (House et al. 1988). Moreover, the benefits of pair bonding and the costs associated with lack of a mate may be greater for men than women (Cramer & Neyedley 1998). Further, the nonrandom pairing of anxious women and avoidant men (Kirkpatrick & Davis 1994) may be extremely beneficial for dismissing-avoidant men. This pairing of dismissing men, who have low levels of caregiving, with anxious women, who are prone to compulsive caregiving, would enable dismissing men to benefit from pair bonding without the cost of having to provide care (Feeney & Collins 2001). Given these considerations, it is not surprising that a substantial proportion of dismissing-avoidant individuals still commit to relationship partners (Bogaert & Sadava 2002), instead of remaining unpaired (although less so than secure individuals).

In summary, we argue that Del Giudice's model ignores the majority of avoidant men, namely, fearful-avoidant men. Moreover, given the limited evidence that dismissing-avoidant men engage in short-term mating strategies, it may not even apply to the subset of men who are dismissing-avoidant. Finally, Del Giudice ignores the benefits of human pair bonding both on, and independent of, reproductive outcomes for dismissing men.

ACKNOWLEDGMENTS
We gratefully acknowledge Cindy Hazan, Melissa Ferguson, Barbara Finlay, Jeanne M. Robertson, and Amanda J. Carreiro for their helpful suggestions on earlier drafts of this commentary.

Author's Response

Human reproductive strategies: An emerging synthesis?

doi:10.1017/S0140525X09000272

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Abstract: In the first part of this response, commentators' critiques to the target article are reviewed and addressed. The main discussion topics are the role of attachment in developmental plasticity; the relationship between attachment, mating, and reproductive strategies; the existence, magnitude, and developmental timing of sex differences in attachment; the adaptiveness of insecure styles; and the neurobiology of attachment and reproduction. The model's assumptions are clarified, and a number of methodological issues that can confound the interpretation of research findings are examined. In the second part, various proposals made by commentators are synthesized, and directions for future research and theoretical improvement are outlined. In addition, the issue of disorganized and fearful attachment is tentatively addressed. It is argued that different theoretical perspectives are converging toward a consistent and comprehensive theory of human reproductive strategies.

Receiving so much feedback is nothing short of thrilling, and the commentators did a great job dissecting my model, criticizing its assumptions, and suggesting novel ways to improve our understanding of human life histories – my thanks to all of them. I am excited at the new opportunities for interdisciplinary integration that are clearly emerging from this lively area of research.

In the target article, I presented an updated evolutionary-developmental model of human reproductive strategies, integrating the life history framework of Belsky, Steinberg, and Draper (Belsky et al. 1991) and Chisholm (1999) with sexual selection and parental investment theory. In this model, insecure attachment in infancy and early childhood entrains reproductive strategies that are based on current reproduction and high mating effort; however, the optimal strategies (and the optimal balance of mating versus parenting effort) differ between males and females. This is reflected in a reorganization of the attachment system in middle childhood, leading to sex differences in insecure attachment styles. In particular, insecure males tend to adopt avoidant styles, whereas insecure females show higher levels of anxiety. In a parental investment/sexual selection framework, sex-specific attachment styles are adaptive both in adults, where they regulate commitment and investment in couple bonding, and in children, where they affect a suite of traits involved in same-sex peer competition. The reproductive strategy adopted by an adult individual is thought to reflect an interplay between early stress and attachment security, genotypic factors, and later experiences (see Fig. 2 of the target article). Finally, I proposed that adrenarche acts as an endocrine switch at the beginning of middle childhood, affecting the sex-specific development of attachment styles and of nascent reproductive strategies.

I begin this response by addressing major criticism, clarifying my model's assumptions, and discussing some methodological issues that had to be omitted from the target article but were often raised in the commentaries (sects. R1–R6). Then, I gather the new suggestions and ideas presented by commentators, and attempt to draw a map of the most intriguing directions for future research (sects. R7 and R8).

R1. Developmental plasticity

The idea that psychosocial stress in infancy and childhood affects the trajectory of reproductive strategies is crucially based on the concept of adaptive developmental plasticity. **Penke** proposes a balanced overview of the place of developmental plasticity among the many mechanisms of evolutionary adaptation. I agree with his presentation in almost every detail, and I concur that the essential question concerns the relative weight of the various mechanisms. Where we disagree is about the significance and weight of attachment, as I discuss further on (sect. R3.1). More radically, **Hönekopp** presents an argument purportedly showing that the plasticity mechanism I proposed cannot work as an adaptation. There are, however, several problems with Hönekopp's argument, concerning both the theoretical reasoning and the evidence cited in its support. First, the small Dogon sample he cites as evidence that attachment is unrelated to mortality was drawn from an atypical, urbanized population, and even so, 23% of the 26 infants were disorganized in 4-way coding (True 1994). Second, the contention that attachment security is insensitive to environmental variation (based on a single review of cross-cultural studies, many of which took place in industrialized countries) is clearly inconsistent with the extreme insecurity proportions found in at-risk and low-socioeconomic status (SES) samples (see references in sects. 2.2 and 2.3 of the target article). Third, an evolutionary perspective challenges the idea that consistently sleeping away from parents is an "irrelevant" variable for infants; in our evolutionary past, losing physical proximity with parents was likely one of the surest signs of danger – not least, because of abandonment risk (Hrdy 1999).

On the theoretical side, the "information chain" presented by **Hönekopp** is based on a partial rendering of my model. In the target article, I argued that environmental risk during infancy and early childhood, strongly mediated by parental behavior, affects reproductive strategies in middle childhood and early adulthood, with the possibility of later revision. Strategic flexibility in adolescence and adulthood (sect. 7.1.3; Fig. 2) makes it unnecessary to accurately predict the environment two decades or so in advance, as implied by Hönekopp; early information channels reproductive strategies in adaptive directions, but it does not "freeze" individuals onto fixed developmental courses. In addition, I tried to stress that parental behavior does not only mediate (macro-) environmental conditions, it also *determines* (micro-) environmental conditions (sect. 7.1.1), thus giving the child direct and valuable information about contingent risk, expected future investment (Ellis 2004; target article, sect. 5.4.1), and alloparental availability.

There are two more reasons why **Hönekopp**'s argument, while interesting, may be overstated. First of all, the information chain he presents is redundant, since the correlations between (1) parental behavior and attachment and (2) attachment and adult reproductive strategy are both controlled by the child, and could well amount to 1.0 if that was in the child's interest. Thus, contrary to the argument's assumptions, there is no *inherent* information loss going from parental behavior to reproductive strategies. Second, acquiring direct and reliable information about environmental risks usually involves exposing oneself to those risks; and while parents are forced to do so, infants and young children should try to avoid direct exposure to danger as much as possible (letting parents do the work for them, so to speak). I agree that children can gain information by observing the environment on their own; but parental behavior (especially when sampled over many years) can still be a useful source of information at various levels, even if we still have a limited understanding of the exact ways in which such information is transmitted and encoded. Mathematical models and simulations could help immensely to clarify this issue (see sect. R7.2).

It is nevertheless true that I did not emphasize flexibility enough (see **Jackson & Ellis** and **Flinn, Muehlenbein, & Ponzi** [**Flinn et al.**]). Reproductive strategies in a long-lived species like ours are most likely implemented by a multi-stage process with a considerable degree of protracted plasticity. The middle childhood transition (for which I propose the label of *juvenile transition*; Del Giudice et al., in press) is only one of the possible "switch points" in human life history, and one of the functions of juvenility may precisely be that of allowing for social feedback about the viability and success of one's strategy (Del Giudice et al., in press). As briefly anticipated in section 7.1, life history models should now move toward a more sophisticated, truly lifespan perspective, integrating the various time frames over which reproductive decisions are made.

R1.1. The role of genetic factors

Developmental plasticity and genetic factors are, in fact, two sides of the same coin (West-Eberhard 2003). Although my present focus was on plasticity, I also stressed that genotypic differences are expected to play multiple and important roles in shaping reproductive strategies. The work on the K-Factor cited by **Figueredo, Sefcek, & Olderbak** (**Figueredo et al.**) is especially interesting, although it would really take too much space to discuss it in detail. I will limit myself to note that Figueredo et al.'s (2004) twin sample was composed of middle-aged people and that heritability could be substantially lower at younger ages, as it happens with other traits (e.g., general intelligence). There are also a number of issues to be considered in order to properly interpret heritability estimates; for example, high heritability may sometimes be compatible with strong causal effects of the environment on a trait (e.g., Turkheimer 2004). Further discussion of how genetic and environmental factors are integrated in the development of reproductive strategies can be found in Del Giudice et al. (in press).

Although behavior genetics can give fundamental contributions to the evolutionary understanding of reproductive strategies, I find **Harris**'s arguments against life history models (and attachment theory in general) to be empirically weak and ultimately unconvincing. First of all, Harris equates non-shared variance in biometric models with extra-familial factors – a problematic interpretation that has been repeatedly challenged (for a thorough discussion, see Rutter et al. 2001; 2006). Moreover, she ignores the consistent findings of low heritability in infants' and children's attachment styles (sect. 2.3). Harris's argument is also weakened by recent, genetically controlled studies linking family stress to age at menarche (Tither & Ellis 2008) and early initiation of sexual activity (D'Onofrio et al. 2006). Importantly, both Tither and Ellis (2008) and Ellis and Essex (2007) controlled for SES in their samples, and the latter also directly controlled for body mass index (BMI); thus, Harris's hypothesis that SES and obesity fully account for the relationship between stress and early maturation doesn't seem to enjoy much empirical support.

R2. How big are sex differences in romantic attachment?

Sex differences in romantic attachment are an essential feature of my model: They are predicted to arise in many human populations, and are thought to result from adaptive processes. In contrast, both **Beckes & Simpson** and **Penke** argue that sex differences in attachment are small, perhaps too small to be of evolutionary significance. This issue deserves a thorough discussion. First of all, my model does not predict generalized, context-independent sex differences in attachment patterns; rather, sex differences should be mostly apparent in *insecurely* attached individuals, and they should peak in moderately risky environments. Since most individuals in most populations are securely attached, overall sex differences in avoidance and anxiety can be expected to be moderate at best. Turning to the empirical size of sex differences in romantic attachment, I concur that there are many inconsistent results in the literature. However, we are likely to severely underestimate the magnitude of sex differences if we fail to take into account four confounding factors: (1) the unreliability of some attachment measures, (2) the restricted nature of most research samples, (3) the effect of age, and (4) the impact of scores distribution on the magnitude of effect sizes.

Of course, to properly address these issues one would need a systematic meta-analysis (currently in preparation); bearing this in mind, in Table R1 I summarize the effect sizes from a number of recent studies. The unreliability of romantic attachment measures is a long-known problem (e.g., Baldwin & Fehr 1995). Unfortunately, many older studies (and some new ones) employ obsolete instruments such as the single-item scales of the Relationships Questionnaire (RQ) (Bartholomew & Horowitz 1991); because of score unreliability, such measures provide downward-biased estimates of sex differences. In addition, the common practice of reducing continuous scores to categories is guaranteed to lose some sex-related variance in the process. At the moment, the best romantic attachment questionnaires are arguably the Experiences in Close Relationships (ECR; Brennan et al. 1998) and the Experiences in Close Relationships - Revised (ECR-R; Fraley et al. 2000); the studies included in Table R1 were selected because they employed one of these measures in the continuous form and reported some measure of association between attachment and sex (note that this is not intended as an exhaustive review, but only as a representative summary of recent studies). All effect sizes were converted to Cohen's d.[1]

Table R1. *Effect sizes of sex differences in romantic attachment (ECR scores) in community and college samples. Positive values indicate higher scores in males.*

	Sex differences (d)	
Study	Anxiety	Avoidance
Community samples		
Watson et al. (2004)	−.40	.24
Brassard et al. (2007)	−.28	.14
Birnbaum (2007)	−.19	.21
Butzer & Campbell (2008)	−.04	.25
Godbout, Lussier & Sabourin (2006)	−.25	.14
College samples		
Crawford et al. (2006)	−.15	.36
Schwartz et al. (2007)	.17	.23
Noftle & Shaver (2006)	−.02	.00
	−.15	.12
Picardi et al. (2005)	−.33	−.11
Gentzler & Kerns (2004)	−.04	−.19

Even a casual review of the literature suggests that sex differences tend to be stronger and more consistent in community samples compared with samples of college students, which are likely to show restricted variability in many life-history-relevant characteristics (such as early family stress, present vs. future orientation, and so on).[2] Note that some of the community samples (Birnbaum 2007; Butzer & Campbell 2008; Godbout et al. 2006) included a substantial proportion of middle-aged participants; and, as I tentatively showed in section 4.3, there seems to be an age-related decrease in the magnitude of sex differences, consistent with the proposed role of sex hormones. Most of the college samples were composed of psychology students; if my hypothesis is correct and gender-typicality is associated with attachment (sect. 7.2.2), then psychology students would provide an especially poor benchmark for estimating population sex differences. Psychology is a strongly female-biased faculty, and males enrolled in psychology courses are likely to represent a restricted segment of an already restricted subpopulation. Preliminary evidence supports this possibility: In a sample I just collected, composed of 200 Italian students from a wide range of faculties (e.g., psychology, humanities, engineering, mathematics, law, and so on), sex differences in ECR scores were $d = -.37$ (anxiety) and $d = .14$ (avoidance) in the psychology subsample ($N = 74$), and $d = -.52$ (anxiety) and $d = .43$ (avoidance) in the rest of the sample.[3]

Another factor that may lead to underestimating sex differences is the non-normal distribution of attachment scores. With skewed or otherwise non-normal data, d (the standardized difference between means) can underestimate the size of group differences. For example, in the student sample described above the overall sex difference in avoidance was $d = .29$, which some may automatically interpret as "small"; but, due to skewed distribution in females, 74% of males showed higher avoidance scores than the median female (hardly a trivial effect). Differences in score distributions can be effectively analyzed using specific statistical methods (e.g., Handcock & Morris 1999); these methods should be employed much more often, especially when dealing with group differences involving non-normal variables.

To conclude, I concur with **Symons & Szielasko** that documenting sex differences in attachment is only the first step, and that sex-specific patterns of correlations should be systematically investigated. Unfortunately, too much attachment research still ignores or downplays the existence of sex differences, so that the relevant analyses are seldom performed (**Kerns**); I hope that the present work contributes to a wider appreciation of this crucial issue.

R2.1. Cultural variation

Although many studies (mostly carried out in Western countries) show evidence of sex differences in romantic attachment, life history models do not predict universal, context-independent sex differences (see Schmitt 2008). As discussed in section 7.1.3, the magnitude of sex differences is expected to be contingent on environmental risk; moreover, **Quinlan** suggests that sex-specific patterns of risk and parental bias could also have important effects. In the cross-cultural study by Schmitt et al. (2003a; 2004), East Asian samples showed small sex differences in dismissiveness and high preoccupation scores; this pattern appears to be mirrored in the Chinese data presented by **Li, He, & Li** (**Li et al.**). However, reanalysis of continuous ECR scores from their original data sets (Li, personal communication, July 7, 2008) shows that, in Chinese college students (from mixed faculties), sex differences go in the same direction as of those observed in Western samples, with higher male scores in avoidance ($d = .26$) and somewhat higher female scores in anxiety ($d = -.12$). In Li et al.'s data on white-collar workers, Chinese men report higher scores in both avoidance ($d = .39$) and anxiety ($d = .24$; details available from the author). Overall, it is possible that sex differences in attachment anxiety are reduced in Chinese people, although it would take a targeted meta-analysis (and more community samples) to put this hypothesis on firmer ground.

Provisionally taking these data at face value, the really interesting question is why East Asian samples should show this kind of pattern, which is not accounted for by my model. Some of the explanations proposed by **Li et al.** (e.g., government-imposed limitations on the number of children) are dubious from an evolutionary point of view. For example, the one-child policy has been implemented only from 1979, and if male reproductive strategies have evolved over phylogenetic time, such recent limitations on reproductive rate are not expected to have a strong effect on male psychology. In addition, similar distributions of attachment scores are found in nations (e.g., Taiwan, South Korea) where there is no equivalent policy (Schmitt et al. 2003a; 2004). These authors may be right, however, when they point to the high sex ratio (more males than females) resulting from preferences for male children.[4] High sex ratios (and preferences for male offspring) are found in many East Asian countries (e.g., South Korea, China, Taiwan; see Coale & Banister 1996; Schmitt 2005b). When reanalyzing the data by Schmitt (2005b; Schmitt et al. 2003a; 2004), I found that high sex ratio in a cultural region predicted higher dismissing (partial $\beta = .29$: $P = .048$, controlling for age) and (especially) preoccupied attachment (partial $\beta = .36$; $P = .011$, controlling for age). In high-sex-ratio populations, males compete to marry the few available females, the mating system tends towards high relationship stability, and sociosexuality is restricted (Schmitt 2005b); one could hypothesize that, in this context, increased anxiety in males might be adaptive by helping maintaining an exclusive bond with females. Although I did not explicitly include the sex ratio in my model, it could be that it affects adult attachment in yet unknown ways; the mechanisms linking sex ratios to attachment and their interaction with environmental risk constitute a fascinating topic for future research.

From a more speculative perspective, it is also possible that population-level differences in attachment are influenced by local differences in neurophysiological parameters and genetic background. The dopamine receptor D4 7-repeat allele, for example, has been implicated in the development of disorganized attachment (see Belsky et al. 2007a; van IJzendoorn & Bakermans-Kranenburg 2006). Strikingly, this genetic variant, relatively common in Europe and Africa, and even more so in South America, is virtually absent in Asian populations (Chang et al. 1996). Other studies indicate that the 7-repeat allele has a recent evolutionary origin (about 50,000 years ago) and that it has been subject to intense positive selection (Ding et al. 2002; Wang et al. 2004); moreover, some authors have proposed that selection on the 7-repeat allele could have been driven by population differences in mating systems and reproductive strategies (Harpending & Cochran 2002).

Given that, in my model, sex hormones have a crucial role in the development of sex differences in attachment, it is also of interest that Asian populations tend to have relatively low androgen levels (for references, see Wang et al. 2007). This effect seems to depend, at least in part, on dietary factors (e.g., Santner et al. 1998), though social factors may also play a role; for example, through a low emphasis on competition in collectivistic societies (see Mazur & Booth 1998). However, recent studies have also documented ethnic variation in a number of genes involved in the sex steroids pathway (Kardia et al. 2006). More research is needed to evaluate this intriguing possibility and to fully work out its evolutionary implications; interestingly, both the distribution of *DRD4* alleles and the data on androgens could point to stronger selection for long-term, biparental care in Asian populations, which would be consistent with less sexually dimorphic attachment patterns (see Harpending & Cochran 2002).

R2.2. Are there sex differences in middle childhood?

Bakermans-Kranenburg & van IJzendoorn present a meta-analysis of sex differences in middle childhood and early adolescence. I especially welcome their hands-on approach and the new data they present; however, their analysis suffers from a number of limitations that make it a poor test of my specific predictions. On the other hand, it also provides a perfect illustration of the subtle issues involved in testing the idea of a hormonally driven reorganization in attachment patterns.

The first issue is that of age. The studies showing significant sex differences presented in section 4.2 all involved children aged 7 years or older; I reported only one study of 6-year-olds (Toth et al. 2006), but I did so in a tentative way and stressing that the effect was smaller, however suggestive. In section 4.1, it was explicitly stated that studies with children as old as six usually fail to detect sex differences. Thus, the fact that three of the studies included in **Bakermans-Kranenburg & van IJzendoorn**'s meta-analysis involve 6-year-old children (Toth et al. 2006; Bureau et al. 2006; Gloger-Tippelt et al. 2007) predictably reduces the overall effect size.

However, age itself is not the whole story, because determining when attachment patterns become sex-biased requires careful consideration of the hormonal mechanism of adrenarche. In my model, I hypothesized that adrenarche drives the re-organization of attachment patterns. Indeed, adrenarche is the biological marker of juvenility (Bogin 1999; Locke & Bogin 2006): this implies that, just as with puberty, the juvenile transition should not be tied to a specific age, but rather, be considered as a dynamic and variable process (Del Giudice et al., in press). Adrenarche starts around 6 years of age for early-maturing children and, at age 7 years, about 50% of children have actually reached adrenarcheal state (Ellis & Essex 2007).[5] To further complicate things, the timing of adrenarche is likely to be geographically and ethnically variable, just as that of puberty. In particular, sexual maturation is slower in northern Europe compared with southern Europe and the United States: while the mean age of menarche is 12.0 years in Italy and 12.5 years in the United States, it is 13.2 years in the Netherlands and 13.5 years in Germany, about one year later (Parent et al. 2003). Assuming (as is reasonable in absence of targeted studies) that adrenarche shows a similar time lag, sex biases in attachment patterns may not be noticeable in Dutch and German samples until about age 8 years or so. Since three of the samples in **Bakermans-Kranenburg & van IJzendoorn**'s meta-analysis are from the Netherlands (Gilissen et al., in press: 7 year-olds; Pannebakker 2007: 7 year-olds) and Germany (Gloger-Tippelt & Konig 2007: 6 year-olds), it is quite possible that most of these children were in fact pre-adrenarcheal. In summary, any meta-analysis targeted at properly testing the developmental hypothesis proposed in the target article should explicitly take into account three key factors: (1) children's age, (2) geographic variation in maturational timing, and, when appropriate, (3) local variation in environmental risk (sect. 7.1.3).

The last issue is that of differences between measurement instruments. As acknowledged in section 4.3, sex differences in adults are only apparent with romantic attachment measures, and (as also shown by **Bakermans-Kranenburg & van IJzendoorn**) do not emerge with state-of-mind interviews like the Adult Attachment Interview (AAI). Explaining why this is so is a fascinating puzzle, and I hope that future research will provide a fully satisfying answer. However, many attachment researchers agree that interviews and questionnaires measure distinct attachment-related constructs (e.g., Bartholomew & Shaver 1998; Bernier & Dozier 2002; Carnelly & Brennan 2002); they also tend to predict different outcomes, both in couple relationships (e.g., Roisman et al. 2007) and in psychopathology (e.g., Fortuna & Roisman 2008). I want to stress once more that AAI-like interviews focus on past attachment relationships and are mostly rated according to narrative qualities (e.g., coherence); that is, they assess the way people talk about their past experiences. The study by Ammaniti et al. (2000) included in Bakermans-Kranenburg & van IJzendoorn's meta-analysis used the Attachment Interview for Childhood and Adolescence (AICA), which is based on the same principles and asks questions such as: "Tell me about your relationship with your parents as a little child." It is quite possible that the way children and adults talk about past relationships does not show sex differences, whereas their attitude towards current attachment figures does. Unfortunately, since Bakermans-Kranenburg & van IJzendoorn take the AAI to be the "gold standard" of adult attachment measures, they choose to ignore the data from questionnaire studies (in children as well as in adults). They also speculate that sex differences in doll-play tasks may be an artifact caused by differences in verbal abilities; however, it is difficult to see how this would account for the observed sex differences in forced-choice questionnaires such as the Coping Strategies Questionnaire (CSQ) (sect. 4.2).

R3. Attachment and reproductive strategies

In the target article, attachment patterns are presented as an integral component of adaptive, sex-specific reproductive strategies. This crucial relationship is the focus of many commentaries and of some critical appraisals. **Penke** and **Petters & Waters** question the general relationship between attachment and fitness-relevant traits and behaviors; **Zayas & Ram**, **Campbell**, and **Chen & Li** raise doubts on the adaptive nature of specific attachment patterns. I am not surprised that the link between attachment and reproductive strategies has turned out to be the most controversial part of my article. Attachment theorists have largely drifted away from Bowlby's original emphasis on evolutionary biology, thus making it difficult to reintegrate many attachment-related concepts and models with modern evolutionary theory. For the same reason, empirical research on attachment often focuses on variables that lack clear biological relevance, or (even more often) concentrates on psychological well-being while neglecting potentially fitness-relevant behaviors. This state of affairs demands special care in properly evaluating the relevant empirical findings. Although I argue that the extant data support the essential lines of my model, there is clearly need for more (and more biologically meaningful) evidence to settle some of the most burning empirical issues.

R3.1. The relationship between attachment, sociosexuality, and behavior

This critical issue easily lends itself to misunderstandings and confusions. Attachment has two separate roles in my model: In infants and children, it "encodes" environmental risk and parental investment, thus contributing to direct the development of reproductive strategies; in older children and adults, it is one of the traits that implement a given reproductive strategy at the behavioral level. In particular, attachment styles contribute to some aspects of behavior (e.g., aggression, self-esteem) in juveniles, and mediate the regulation of intimate couple relationships in adults (e.g., emotional commitment, investment, and requests for investment; sect. 6.3.1). Two important implications follow: (1) attachment styles are not the "cause" of all the behavioral manifestations of life history strategies; (2) the specific effects of attachment in adults primarily concern the formation, maintenance, and regulation of long-term relationships, and only secondarily the regulation of short-term sexual relationships (unfortunately, the distinction was somewhat blurred in sect. 5.2).

Although the standard approach to sociosexuality sees long- and short-term relationships on a bipolar continuum (see Simpson et al. 2004), things are probably much more complex. As Jackson and Kirkpatrick (2007) showed, mating strategies (already a subset of reproductive strategies) can be mapped on at least two distinct dimensions, with possible overlap and tactical admixture between the pursuit of long-term relationships and short-term sexual affairs (see also sect. 6.4.1). For example, "sexually unrestricted" females are nevertheless highly sensitive to partners' willingness to invest, tend to feel emotionally vulnerable after intercourse, and feel distressed if their partner fails to show involvement (Townsend 1995; 2005).

Until recently, most researchers have focused exclusively on short-term mating, usually measured with the Sociosexual Orientation Inventory (SOI; Simpson & Gangestad 1991). Based on the evidence reviewed in my article, however, attachment can be expected to prove much more predictive of attitudes, desires, and behaviors related to intimate, committed relationships (see Jackson & Kirkpatrick 2007 for promising results). There is absolute need of instruments assessing "long-term reproductive behaviors," that is, actions that promote couple stability and channel investment within the monogamous couple (a good example is the Partner-Specific Investment Inventory by Ellis [1998]). Natural selection is not only a matter of individual fertility: offspring quantity and quality both contribute to long-term fitness (**Ackerman & Kenrick**; Houston & McNamara 1999), and tracking the dynamics of parental investment is just as important as tracking the number of one's mates.

That said, I still think that **Penke**'s contention that "there seems to be surprisingly little evidence that romantic attachment styles actually relate to reproductive strategy-related consequential behavioral outcomes" is overstated, even with respect to short-term mating. First, he ignores the available evidence on casual sex, age of intercourse, infidelity, and sexual coercion (see sect. 5.2 in the target article and earlier here). Then, he challenges the significance of attachment on the grounds that attachment styles only predict "sociosexual attitudes," which do not uniquely correlate with (short-term) behavioral outcomes. However, in their own research, Penke and Asendorpf (in press) found that attachment also correlated with "sociosexual desire," which in turn did predict a number of interesting reproduction-related behaviors. Considering that they employed the single-item RQ, Penke's dismissal of attachment may be premature. Finally, when evaluating the size of correlations one must be wary of some possible statistical artifacts. As discussed earlier, attachment scores may present with skewed distributions; the same is true of sociosexual measures (e.g., Jackson & Kirkpatrick 2007) and of reports of relatively infrequent behaviors (e.g., infidelity, sexual coercion). Pearson's correlation assumes normally distributed variables, and correlation coefficients can be deflated when one or both variables are skewed. If researchers do not take the appropriate statistical steps (e.g., transforming the data or computing rank correlations), they can end up underestimating the size of associations.

In a similar vein, **Petters & Waters** argue that correlations between attachment styles and behavioral traits like aggression or withdrawal are "very small or inflated by considerable method variance." It is true that correlations are sometimes small (e.g., consistently around .2 in Finnegan et al. 1996), but this is not always the case; for example, Granot and Mayseless (2001) reported a threefold increase in externalizing symptom scores between the secure and avoidant attachment groups (together with other effects of similar magnitude). In both of these studies, shared method variance was not an issue, as attachment was assessed by self-report or doll-play and the other measures came from teacher and peer reports. Skewed distributions (see earlier) may also contribute to deflating effect sizes in some of the studies. At a more fundamental level, I propose that employing more ecologically relevant variables and categories (e.g., dominance-seeking and relational aggression instead of "externalizing behaviors") is likely to yield stronger and more meaningful correlations.

To conclude this section, I want to address **Petters & Waters**'s suggestion that attachment may not be crucial to my model, and that I should focus on the direct relationship between early stress and later reproductive behavior. In short, I don't think that such a direct relationship exists: although my focus is on reproductive strategies, attachment relationships are the primary source, filter, and buffer of stress for the child (e.g., Flinn 2006). Thus, it is difficult even to conceptualize early stress without considering attachment. At the same time, attachment is crucially involved in human pair-bonding, so that a full understanding of the dynamics of parental investment cannot sidestep adult attachment styles. Any theory of human reproductive strategies must deal with attachment, one way or the other.

R3.2. Are insecure patterns adaptive?

While accepting the general lines of the target article's evolutionary framework, some commentators disagree about the specific adaptive function of insecure attachment patterns. **Zayas & Ram** argue that neither avoidance nor short-term mating are adaptive for males; **Campbell** doubts that attachment anxiety can help females in eliciting male investment, and **Chen & Li** believe that avoidance should be more adaptive for females than anxiety.

Zayas & Ram take issue with the view that male avoidant attachment is part of an adaptive reproductive strategy, and cite a number of findings concerning the lack of correlations between avoidance and frequency of intercourse, age at first intercourse, and extra-pair affairs. The first study they cite is Tracy et al. (2003); this study, however, was based on the same data set of Cooper et al. (1998), which was already criticized in section 5.2 for employing an unreliable measure of attachment, likely to misclassify as dismissing many fearful subjects, who indeed show a peculiar pattern of sexual behavior (see sect. R8). Second, they cite Bogaert and Sadava (2002), who found no relationship between avoidant attachment and infidelity; however, in another study, Allen and Beaucom (2004) reported that dismissing males had had the highest number of extra-dyadic partners. Avoidance also predicts reduced sexual fantasies about the current partner (Brassard et al. 2007) and greater romantic attraction to potential alternative partners (Overall & Sibley 2008).

Taken as a whole, the evidence is not as negative as implied by **Zayas & Ram**; of course, the relevant studies are still a handful, and more data are needed to firmly settle this issue. Third, I agree that avoidance predicts lower frequency of intercourse, but intercourse frequency has little to do with short-term mating; if anything, one should expect a negative correlation between partner variety and intercourse frequency, as already discussed by Brody and Breiterstein (2000) and Simpson et al. (2004). Looking for new partners and getting to have sex with them takes time, with a resulting trade-off between variety and frequency; and if frequent intercourse with a partner can strengthen a couple's relationship and increase intimacy (e.g., Costa & Brody 2007; Mellen 1981), people engaging in low-commitment strategies should have sex with their partners less often in order to maintain a low level of intimacy. Reduced intercourse frequency may, ironically, reflect an adaptive aspect of low-investment strategies.

Another argument used by these authors to challenge the adaptiveness of casual sex is that frequent intercourse within a stable pair-bond increases the likelihood of fertilization and, therefore, reproductive success. This fails to take into account the evidence that women tend to engage in extra-pair sex precisely in their phase of maximum fertility (see **Volpe & Barton**). Concerning their argument that pair-bonding increases reproductive success because it promotes parental investment in offspring, I wholeheartedly agree: but my model predicts that males will shift to avoidant strategies precisely when there are cues of risk, that is, when parental investment is *less likely* to benefit offspring (sect. 6.3.1). While **Zayas & Ram** may be mixing proximate and ultimate causation when they refer to the "psychological and social benefits" of pair-bonding, they make an interesting point when they cite evidence of health-related benefits, which could have nontrivial fitness effects. Also in this case, however, their logic ultimately turns out to support my model: for if intimate pair-bonds have beneficial health effects, the latter are likely to be reaped in the long term and only when the environment is not too risky. In risky environments, the optimal behavior is to trade long-term fitness benefits (including the health-promoting effects of close relationships) for current reproduction, which is precisely what avoidant males are doing in the model.

Finally, **Zayas & Ram** are correct in writing that I neglected fearful attachment in my article. In many respects, fearfulness (high avoidance plus high anxiety) is a puzzle similar to that of disorganized attachment, and the two may actually be related (Simpson & Rholes 2002). Further on, I address this issue in a preliminary way (sect. R8).

The hypothesis that anxious attachment in females is part of an adaptive, investment-eliciting strategy is challenged by **Campbell**, mostly on the basis of research showing correlations between attachment anxiety and violence toward partners. Unfortunately, nearly all the evidence she cites is from studies of borderline personality disorder (BPD). But attachment anxiety is not, as Campbell states, "a short step [. . .] to the clinical condition of borderline personality disorder"; the latter is a serious condition with an incidence of about 2% (see *Diagnostic and Statistical Manual of Mental Disorders*, 4th edition, Text Revision, American Psychiatric Association 2000), whereas anxious attachment is a non-clinical trait with high frequency in normal samples. In addition, BPD appears to be strongly related to fearful attachment (see sect. R8), rather than just anxiety (Brennan & Shaver 1998; Goldenson et al. 2007). The only non-clinical study of violence cited by Campbell is that by Orcutt et al. (2005), who reported an association between anxious attachment and female violence against partners. However, a closer look at their results reveals that the great majority of reported violent acts was composed of minor assaults such as "grabbed partner," "slapped partner," and "threw something at partner that could hurt him/her," and engaging even once in any of these behaviors had participants classified as "violence perpetrators." Despite these behaviors' unpleasant nature, they don't seem likely to end a romantic relationship. Indeed, they could help in *maintaining* a relationship if triggered by the feeling of being neglected by one's partner; and, if triggered by jealousy, in dissuading him from engaging in extra-pair activities (i.e., securing exclusive investment).

Anxious people require high levels of emotional support by their partners, over-attribute rejection during conflicts, and tend to escalate conflictual episodes (Campbell et al. 2005); in this context, aggression and escalation may be directed precisely at preventing rejection. Thus, although I don't think that **Campbell**'s critique undermines the logic of my model, I thank her for pointing to an omission in my account: namely, the role of anger and aggression in the relational style of attachment-anxious people. Ambivalent infants and children often alternate submission and dependency with bouts of anger toward their attachment figures, and the expression of anger is considered as an integral component of their attachment pattern (Ainswort et al. 1978; Cassidy & Berlin 1994); data like those by Orcutt et al. (2005) suggest that anger may have a similar role in adult relationships as well, though more focused research is clearly needed.

Campbell then points out that, if ambivalent girls are preparing to compete for access to male investment, they could be predicted to show higher "direct or indirect" aggression toward peers. This is a well-taken point; and although extant evidence indicates that ambivalent girls engage in less physical/direct aggression with peers (Corby 2006; Finnegan et al. 1996; Granot & Mayseless 2001), I am aware of no specific data on relational aggression. Because commonly employed measures of externalizing symptoms are heavily biased toward direct aggression, it may well be that researchers have been missing a piece of the puzzle, and that ambivalent girls do engage in more relational aggression with their friends. The higher level of anxious/depressive symptoms they experience could partly follow from the resulting stress in peer relationships.

Distinguishing between direct and relational aggression may also be the key to answering the argument put forward by **Chen & Li**, who reason that avoidance should benefit girls and boys alike because (1) in high-risk conditions aggression can be adaptive, and (2) avoidance, but not anxiety, predicts aggression in children. Indeed, all the studies they cite measured direct and/or physical aggression, which is less typical of girls and probably less adaptive in female peer groups under most conditions. I also think that Chen & Li's position is actually more similar to mine than they acknowledge: They state that "the behavioral correlates of avoidant attachment [. . .] are more adaptive than traits associated with ambivalent attachment [. . .] under extreme high-risk environmental conditions." But that is fully consistent with my model: I also predict that, under *extreme* risk, females will shift toward avoidance, while ambivalence should be preferred in conditions of moderate risk (sects. 6.3.1 and 7.1.3). In any event, there are differences between boys and girls in the key resources they need and in the ways they acquire them (**Jackson & Ellis**); we need further research to understand the possible roles of ambivalence in the context of girls' developmental trajectories. While **Goetz, Perilloux, & Buss** (**Goetz et al.**) make the plausible point that the primary evolutionary targets of ambivalence in middle childhood are parents (see also sect. 6.3.1), their statement that girls' social networks are too volatile to last into adulthood may not have been true in ancestral environments (or even in small-scale traditional societies, where choice of friends is severely limited by the small number of same-aged peers).

Campbell also questions the adaptive nature of avoidant attachment in females by suggesting that avoidance may be a forced option in absence of men able or willing to invest, and may not involve devaluing stable relationships. Research suggests that avoidant females, at least in college samples, do tend to devalue stable relationships and to deny that they are interested in them (Jackson & Kirkpatrick 2007). The gang girls described by Campbell sound as if they are fearfully attached, rather than just avoidant; nevertheless, reproductive strategies can change following environmental feedback (sect. 7.1.3), and the commentary by **Kang & Glassman** anecdotally suggests that some homeless girls may shift from "hopeful" anxiety to avoidance when they repeatedly fail to establish a viable relationship. Whether this represents temporary reproductive suppression or an escalation in perceived environmental risk is a question for future systematic research. In the end, the observations by Campbell and Kang & Glassmann reinforce my hypothesis that female avoidance is a heterogeneous construct, and that it may reflect different kinds of underlying strategies (sect. 6.3.1); I think we are still a long way from fully understanding the development of avoidance in women.

R4. Attachment, reproduction, and neurobiology

In section 6.3.1, I speculated that women may sometimes experience reproductive suppression, and that this might correlate with shifts in attachment styles (e.g. temporary increases in avoidance). **Seltzer & Pollack** argue that I made a careless comparison with primates, among which suppression is induced in helpers by the presence of reproducing dominants; they then contend that humans lack specialized physiological mechanism capable of suppressing fertility. Wasser and Barash (1983) were the first to propose that human females may undergo reproductive suppression following lack of social support and/or aggression by other females. Leaving aside the purely terminological issues, I don't think their hypothesis ignores the complexities of comparative biology; in a way, Seltzer & Pollack may themselves be drawing too quick a parallel between cooperative breeding in humans and in other primates. Remarkably, in the human breeding system, helpers are frequently older and more dominant individuals (e.g., grandparents, aunts); thus, the common pattern of dominant-induced reproductive suppression may rightly fail to apply to humans, and a differently tuned mechanism may be present. Moreover, Seltzer & Pollack's contention that humans lack the necessary fertility-reducing mechanisms is not warranted: there is evidence that social stress can affect reproduction in human females by reducing ovarian function, delaying ovulation, inducing spontaneous abortions and premature births (and, not least, by increasing the likelihood of abandonment or infanticide). For references, see Wasser and Barash (1983), Wasser (1994), Wasser and Place (2001), Hrdy (1999), Arck et al. (2001), and Sanders and Bruce (1997); see Ellison (2001) and Vitzthum (2008) for a discussion of "graded" fertility regulation in women.

I am also more optimistic than **Seltzer & Pollack** about the possibility of linking adult attachment to a relatively clear neurobiological basis. While human romantic attachment is in many respects a unique trait, it is not "seemingly unrelated to the physiological mechanisms of social behavior studied in other species." For example, romantic attachment anxiety has been recently linked to increased oxytocin (OT) levels (Marazziti et al. 2006) and heightened cortisol reactivity (Quirin et al. 2008) – two variables with clear relevance to comparative models of pair-bonding. Speaking of oxytocin, I appreciate the suggestion by **Chen & Li** that this hormone may be crucially involved in the development of female (and, I think, male) attachment styles. I also agree that avoidant attachment is probably linked to low OT levels, and believe that the regulation of OT by sex hormones may be one of the causal mechanisms through which adrenarche affects attachment behavior (see also Campbell 2008a; **Goldstein Ferber**'s commentary). They probably go too far, however, when they argue that OT has little or no effect on the adult brain: As recent experimental studies demonstrate, OT administration in adult humans can have remarkable effects on social perception and behavior (e.g., Domes et al. 2007; Guastella et al. 2008; Kosfeld et al. 2005; Zak et al. 2005). In addition, it is often difficult to know for sure whether or not OT receptors are expressed in a given brain region (see Gimpl & Fahrenholz 2001).

The physiology of stress is also at the heart of **Goldstein Ferber**'s commentary, where the proposal is made that prenatal mother–fetus interactions may prime the subsequent development of attachment and sex differences. I basically agree with Goldstein Ferber on this point (see Fig. 2), although her evolutionary reasoning appears somewhat obscure when she discusses costly signaling and the handicap principle. Finally, **Petters & Waters** remark that, while physiological factors can partly mediate the effects of the environment on attachment, adaptive processes can be mediated by cognitive processes as well. I totally agree with them, but different processes require different types of mechanisms: and when it comes to coordinating sexual maturation, reproduction, motivation, and social behavior (as life history strategies imply), there really is no alternative to hormones and their powerful integrative function (**Flinn et al.**). See Del Giudice et al. (in press) for an extended discussion of this topic.

R5. Sex differences in mating versus parenting effort

I now address a problematic aspect of the target article that was not singled out by commentators. In order to derive sex-specific predictions about life histories, I relied on Trivers' Parental Investment Theory (Trivers 1972). I was unaware that, a few years before, Trivers' famous model had been shown to embed a number of fallacies, one of which I imported straight into my own article. In short, the assumption that males enjoy (on average) a higher fitness gain than females for a given investment in mating effort (sect. 6.3.1) is inaccurate, because, with an even sex ratio, the average reproductive success of males and that of females have to be equal by arithmetic necessity (see Kokko & Jennions 2003; 2008). This fallacy is not fatal to the model, but it requires further specification and a more complex set of assumptions. For example, investing in mating instead of parenting can be an optimal strategy for males, provided that they can reliably assess their own mating potential and adjust their strategy accordingly (Kokko & Jennions 2008; Kokko, personal communication, April 9, 2008).

What are the consequences for my theory? First, this is one more reason to call for a multi-stage model with repeated sequences of strategic decision-assessment-adjustment (sect. R1). My hypothesis is that juvenility and adolescence (**Symons & Szielasko**; **Jackson & Ellis**) are especially useful as self-assessment phases (Del Giudice et al., in press). Second, the importance of self-assessment broadens the theoretical rationale for including phenotypic quality and social feedback in life-history models (Jackson & Ellis). Third, for some males (those of uncertain mating potential) who adopt avoidant strategies, the optimal tactic would not be that of eschewing parenting effort altogether; rather, these males should be more willing to cut on parenting effort and invest in mating when mating opportunities arise. The evidence that avoidant people are less involved in current relationships and more easily "tempted" by potential alternative partners (e.g., Brassard et al. 2007; Overall & Sibley 2008) is intriguing when viewed in this light. Of course, these considerations apply all else being equal; for example, unbalanced sex ratios can considerably alter the costs and benefits of different strategies, and so on.

R6. Miscellaneous topics

A number of specific comments and critiques were made by **Figueredo et al.**; I address them in turn here. With respect to the assessment of attachment, I also side with the continuous/dimensional measurement camp. I am not sure, however, that two dimensions are enough: in particular, fearful attachment may possess some qualitatively different properties, and they may be better captured by a specific scale (see sect. R8). As for the misstated sentence in section 3.1, its intended meaning is that the fitness contribution of a given trait must be weighted – costs and benefits – over the whole lifetime of an organism. Figueredo et al. are also puzzled by my discussion of age-related shifts toward paternal investment and by my (schematic) analysis of polygyny. Concerning the former, I see no particular contradiction: as discussed above (see sect. R3.1), short-term mating is only a single facet of reproductive strategies, and (depending on various social and personal factors) it can coexist with variable degrees of investment in long-term relationships and in offspring care. With respect to polygyny, the literature on human mating systems is complex and, alas, sometimes contradictory; however, in contrast to what Figueredo et al. argue, there is evidence that in polygynous systems, paternal involvement is reduced (Quinlan 2007) and males contribute in smaller proportions to family subsistence (Marlowe 2000; 2003).

R7. Emerging perspectives

Many commentators proposed ways to advance, extend, and specify the model presented in the target article; I found their comments to be exceptionally inspiring and stimulating. Such a high degree of convergence does not happen by chance: It seems to me that a new, comprehensive theoretical synthesis on human reproductive strategies is just within reach (**Ackerman & Kenrick**; **Jackson & Ellis**; **Beckes & Simpson**; **Goetz et al.**). Here I shall try to show how a number of empirical and theoretical threads are coming together, and how this could help in shaping future research in the field.

R7.1. Theoretical integration

Reproductive strategies are not just another facet of human behavior; they lie at the very heart of developmental processes and have implications for a wide range of psychological phenomena, including some that may at first sight seem unrelated (**Ackerman & Kenrick**). It is not surprising, then, that understanding them requires multiple levels of analysis and a confluence of different evolutionary approaches. In the target article, I tried to work on the life-history side of the topic, and I am glad that commentators responded by making explicit some of the links I hinted at in section 6.4. I find **Jackson & Ellis**'s complementary approach exciting, and I believe that their focus on social competition and phenotypic quality hits the target. Indeed, I reached a parallel conclusion when adjusting my model to avoid unrealistic assumptions about reproductive success (see sect. R5); this strongly suggests that the theory can be made fully consistent once we reach a sufficient level of detail.

My view (in agreement with **Jackson & Ellis**, **Flinn et al.**, and **Goetz et al.**) is that we need a multi-stage theory, with multiple decision-assessment-adjustment phases focused on different cues at different points in development. Of course, more research (theoretical as well as empirical) is needed to gain a fuller appreciation of which cues are important and how they are conveyed – a point beautifully made by **Beckes & Simpson.** I agree with them that different risk factors call for different strategies, and differentiating pathogen stress from interpersonal conflict is a good place to start; I have only a few minor reservations on their present account. First, a non-obvious possibility is that the levels of attachment-related stress already contain some implicit information on the likely sources of risk, especially when both parents are considered (sect. 6.2.1). Second and related, the specific consequences of pathogen load may depend on its severity. In a life-history perspective, the crucial question is whether parental effort is repaid by offspring fitness or not; at moderate levels of pathogen stress, increasing parental care may work better than withholding it (see Quinlan 2007). Third, different sources of risk are likely to covary, as suggested for example by the association of polygyny with pathogen stress (e.g., Quinlan 2007), thus making tests of independent effects more difficult.

Beckes & Simpson and **Volpe & Barton** point to another issue neglected in the target article – that of mate preferences and mate choice. This is a bridge that needs to be crossed in order to integrate life-history and strategic-pluralism models. Fortunately, there is some promising work in this direction, investigating how attachment styles in women relates to mate preferences (Cohen & Belsky 2008; Kruger 2008). Also in this case, actual behaviors should be assessed in addition to self-reported preferences, but I suspect that the data will ultimately reveal consistency rather than conflict between different theoretical perspectives. A crucial issue in testing hypotheses about mate preferences will be careful consideration of how reproductive strategies relate to mating styles (see sect. R3.1); for example, it is important not to conflate short-term mating (e.g., unrestrictedness at the SOI) with low-investment, present-oriented life histories. Even with this caveat in mind, Volpe & Barton's fascinating suggestion that some components of romantic attachment may fluctuate in parallel with mate preferences during the menstrual cycle is definitely worth investigating.

R7.2. A call for interdisciplinarity

A common theme in many commentaries is the need for a multidisciplinary approach to the development of reproductive strategies (e.g., **Kruger**). One of the beauties of evolutionary theory is that it naturally leads to interdisciplinarity, as masterfully illustrated by Wilson (1998). In addition, a serious interdisciplinary perspective provides abundant constraints on hypothesis-building, thus protecting against just-so-storytelling. Despite what some critics of evolutionary psychology believe, figuring out an adaptive explanation that is simultaneously consistent with the available psychological, anthropological, and neurobiological data (in addition to general evolutionary theory) is *anything* but easy. Of course, theory construction also becomes exponentially harder, and some commentators have rightly pointed at some underdeveloped aspects of my account. I agree with **Maestripieri**, **Seltzer & Pollack**, and **Kruger** on the need for more comparative evidence from other primates, although our reproductive system is probably unique in various respects. Maestripieri provides an excellent rationale for the use of primate experiments in investigating attachment, and his data on girls' interest in infants suggest how to assess life-history hypotheses going beyond the usual focus on mating styles and menarche timing.

The importance of anthropological and cross-cultural data cannot be understated, as I hope to have shown in the target article. **Quinlan**'s brilliant analysis of sex-specific risk and investment patterns illustrates the complex interplay among ecological factors that anthropologists are familiar with, and suggests some directions to formulate new, testable cross-cultural predictions (see also **Lewis & Tooley** for another application of the Trivers-Willard hypothesis). Then, when moving from the functional to the mechanistic level of analysis, it is extremely useful to investigate the neurobiological substrates of behavior (**Maestripieri**; **Goldstein Ferber**; **Seltzer & Pollak**; **Chen & Li**; **Flinn et al.**). True integration of human (and nonhuman) neurobiology with modern evolutionary biology still has a long way to go, although there are signs of accelerating progress. Clearly, both sides are going to greatly benefit from increased interdisciplinarity.

I don't want to convey the impression that I am neglecting the contribution of developmental psychology and, in particular, of attachment research. Despite occasional criticism, I believe that attachment researchers are in an especially favorable position to leave behind psychology's biophobia and contribute to the cutting edge of interdisciplinary research. In this context, **Kerns**'s commentary provides a much needed developmental perspective on attachment dynamics in middle childhood. It is true that the target article concentrated on the functional and neurobiological levels at the expense of the psychological one (see also **Petters & Waters**). But what happens to parenting and parent–child relationships with the transition to middle childhood? And what happens to "internal working models"? Do peers have a proximate role in shaping children's attachment patterns? I am grateful to Kerns for asking these questions, and hope that research will soon provide some answers. The study of attachment development in middle childhood is still at the beginning (but see Kerns & Richardson 2005); hopefully, increased attention to evolutionary questions and models will help researchers to frame their studies in a biologically relevant manner, thus contributing to testing and refining the most interesting evolutionary hypotheses on development.

Finally, I am very positive about the modeling approach proposed by **Petters & Waters.** If anything is lacking from current evolutionary psychology, it is formal mathematical modeling in addition to verbal theorizing. Here, the lag behind evolutionary biology at large is apparent; this forces researchers to rely on general middle-level theories (with loss of specificity), or on models originally developed for other species (with the risk of making unrealistic assumptions). My feeling is that our verbal models (mine included) are already too complex to be fully worked out without the benefit of a formal approach; and if we start adding the many layers of complexity required for realistic and detailed prediction (**Quinlan**; **Beckes & Simpson**; **Goetz et al.**), things are going to quickly become unmanageable. In this context, simulations can provide a useful tool to assess the consistency of theories, discover their most robust predictions, and possibly simplify them in important ways. Most likely, they will also help in understanding what aspects of the environment are really important, and how they can be effectively encoded by the developing child and his/her family (see sect. R1).

R8. The puzzle of disorganized and fearful attachment

One of the main limitations of the target article is that it leaves out of the picture both disorganization and adult fearful attachment (i.e., high levels of both anxiety and avoidance), and some commentators correctly noted this omission (**Figueredo et al.**, **Zayas & Ram**, **Kerns**). The first crucial question about disorganization is whether or not it is adaptive. Apparently, the current consensus lies on the "no" side; and **Lewis & Tooley** present a reasoned argument to the effect that disorganization falls outside the expected caregiving range of humans, and may therefore lead to maladaptive and pathological behavioral outcomes.

On one hand, it is clearly possible that some forms of disorganization may be non-adaptive results of a disruption of the attachment system. On the other hand, there are at least two reasons to look for possible adaptive explanations. First, the resemblance (also noted by **Lewis & Tooley**) of some disorganized behaviors with mammalian defense reactions is probably not a coincidence; and second, the implicit assumption that abuse and severe neglect were more or less unknown in ancestral human families is probably incorrect. For example, Hrdy (1999) provides a sobering evolutionary account of abandonment and filicide throughout human evolution and across cultures; furthermore, step-fathering has probably been frequent in our phylogenetic history (see Miller 2000), and this should have led to recurrent risk of violence and abuse (e.g., Daly & Wilson 1996). For all these reasons (and without any ethical implication), I object to the widespread idea that severe neglect or abuse are outside our species-typical parenting patterns (e.g., Scarr 1992). If the above is correct, it may be that disorganization represents (at least in some cases) an adaptive response to grave and persisting danger, and that its developmental correlates are tuned to the task of surviving through extreme high-risk conditions. The fact that attachment disorganization seems to represent a transitory stage for most children (e.g., Main 2005; Moss et al. 2005) could be regarded as consistent with this position.

What about fearful attachment in adults? The least that can be said is that fearfulness is not a well-understood category. I am sympathetic to Simpson and Rholes's (2002) argument that adult fearfulness may be functionally similar to infant disorganization. However, this would imply that present two-dimensional models of attachment (which do not assess anything resembling disorganization) are probably inadequate to fully capture the functional meaning of fearfulness. Indeed, it can be argued (as Feeney [2002] has done) that we need more than two dimensions to adequately describe adult attachment styles; and evolutionary theory may actually provide the best guidelines for generating new items and scales.

At present, it is likely that romantic attachment questionnaires lump together phenotypically similar but functionally different patterns: for example, if my speculative hypothesis were correct, avoidance in women (with or without high anxiety levels) could sometimes represent a behavioral correlate of reproductive suppression (sect. 6.3.1). Another pertinent example is provided by developmental shifts in attachment styles (**Kang & Glassman**); what happens to anxious girls when they shift toward avoidance following repeated failures to establish a couple relationship? Do they become dismissing (i.e., their anxiety drops) or fearful (i.e., they maintain high anxiety coupled with increased avoidance)? For some individuals, fearfulness may represent a transitory stage, whereas for others it may be a stable condition. It quickly becomes apparent that fearfulness (as presently defined) could be a mixed category, including persons with very different histories and reproductive strategies. This may also account for the bizarre pattern of sexual behavior associated with fearfulness: for example, a close look at the results by Gentzler and Kerns (2004) shows that high avoidance and high anxiety are found in the group of students reporting early intercourse, but also in that of students reporting no intercourse at all. In conclusion, it seems to me that in order to reach a satisfactory understanding of adult romantic attachment, we need (1) more longitudinal studies, both in the long and in the short term, and (2) more sophisticated measurement models that tap on biologically significant attachment-related constructs.

R9. Conclusion

I am glad that the target article has stimulated discussion of so many important themes. My top list of issues worthy of further investigation includes the developmental course of sex differences in attachment; the reasons for cross-cultural variation; the nature of the information transmitted from parents to children; the role and weight of genotypic factors; the flexibility of individual reproductive strategies; the differences between alternative measures of attachment and their developmental correlates; and the meaning of disorganized and fearful attachment. I will be proud if this article contributes even a little to (re)integrating attachment theory with evolutionary psychology; but, as the commentaries make evident, the study of human reproductive strategies already transcends parochial academic boundaries and involves a wide array of interdisciplinary competences. The main message I gather from this exchange is that, despite the multitude of perspectives that bear on this topic, there are striking opportunities for synthesis and complementarity. If the future delivers what the present promises, the study of human development is in for a really exciting time.

NOTES

1. An advantage of converting from r to d is that imbalances in the frequency of males versus females in a sample (extremely common in the attachment literature) lead to smaller point-biserial correlations, thus encouraging downward-biased estimation of sex differences. In contrast, d is unbiased by the relative frequencies of the two sexes in the sample (see McGrath & Meyer 2006).

2. In Crawford et al. (2006), 90 participants were males and 217 were females (Crawford, personal communication, July 10, 2008). These frequencies are needed to calculate d from r.

3. It should also be noted that effect sizes such as Cohen's d must be interpreted case-by-case, depending on the theoretical meaning of the effect, the scale's reliability, and the amount of measurement error. Relying on "canned" effect sizes (e.g., $d = .8$ is "large," and so on) is bad statistical practice and was strongly discouraged (alas, to little effect) by Cohen himself (Cohen 1988; see also Breaugh 2003).

4. The increasing proportion of male children in the last thirty years is probably explained by selective abortion; however, neglect of female children and selective adoption have also been suggested as potential factors, and parents may sometimes omit to register the birth of a girl; see Coale and Banister (1996) and Ding and Hesketh (2006).

5. There are some discrepancies in the literature about the exact timing of adrenarche, as reflected, for example, in **Flinn et al.**'s commentary. I find most convincing the data showing initial adrenal activity at about 6 years (at least in some children), and smaller sex differences in age of onset compared with gonadarche. See section 7.2.1 for references.

References

Letters "a" and "r" appearing before authors' initials stand for target article and response references, respectively.

Abbott, D. H., Saltzman, W., Schultz-Darken, N. J. & Tannenbaum, P. L. (1998) Adaptations to subordinate status in female marmoset monkeys. *Comparative Biochemistry and Physiology, Part C: Pharmacology, Toxicology and Endocrinology* 119(3):261–74. [LJS]

Ackerman, J. M. & Kenrick, D. T. (2008) The costs of benefits: Help-refusals highlight key trade-offs of social life. *Personality and Social Psychology Review* 12:118–40. [JMA]

(under review) Raising and razing romantic relationship barriers: How men and women cooperate in courtship. [JMA]

Ackerman, J. M., Kenrick, D. T. & Schaller, M. (2007) Is friendship akin to kinship? *Evolution and Human Behavior* 28:365–74. [JMA]

Adkins-Regan, E. (2005) *Hormones and animal social behavior*. Princeton University Press. [aMDG]

Adolphs, R. (2003) Cognitive neuroscience of human social behavior. *Nature Reviews/Neuroscience* 4:165–79. [MVF]

Ahnert, L. (2005) Parenting and alloparenting: The impact on attachment in humans. In: *Attachment and bonding: A new synthesis*, ed. C.S. Carter, L. Ahnert, K. E. Grossmann, S. B. Hrdy, M. E. Lamb, S.W. Porges & N. Sachser, pp. 229–44. MIT Press. [aMDG]

Ainsworth, M. D. S. (1989) Attachments beyond infancy. *American Psychologist* 44:709–16. [DKS]

Ainsworth, M. D. S., Blehar, M. C., Waters, E. & Wall, S. (1978) *Patterns of attachment: A psychological study of the Strange Situation*. Erlbaum. [arMDG]

Allen, E. S. & Baucom, D. H. (2004) Adult attachment and patterns of extradyadic involvement. *Family Process* 43:467–88. [arMDG]

Allen, J. P. & Land, D. (1999) Attachment in adolescence. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver, pp. 355–77. Guilford. [aMDG, DKS]

Als, H. (1986) A synactive model of neonatal behavioral organization: Framework for assessment of neurobehavioral development in the premature infant and for support of infants and parents in the neonatal intensive care environment. *Physical and Occupational Therapy in Pediatrics* 6(Special issue):3–55. [SGF]

Als, H., Duffy, F. H., McAnulty, G. B., Rivkin, M. J., Vajapeyam, S., Mulkern, R. V., Warfield, S. K., Huppi, P. S., Butler, S. C., Conneman, N., Fischer, C. & Eichenwald, E. C. (2004) Early experience alters brain function and structure. *Pediatrics* 113(4):846–57. [SGF]

Als, H., Lawhon, G., Duffy, F. H., McAnulty, G. B., Gibes-Grossman, R. & Blickman, J. G. (1994) Individualized developmental care for the very low-birth-weight preterm infant: Medical and neurofunctional effects. *Journal of the American Medical Association (JAMA)* 272(11):853–58. [SGF]

American Psychiatric Association (2000) *Diagnostic and statistical manual of mental disorders*, 4th edition [Text revision]. American Psychiatric Association. [AC, rMDG]

Ammaniti, M., Van IJzendoorn, M. H., Speranza, A. M. & Tambelli, R. (2000) Internal working models of attachment during late childhood and early adolescence: An exploration of stability and change. *Attachment and Human Development* 2:328–46. [rMDG, KAK, MJB-K]

Anderson, P. J. & Doyle, L. W. (2008) Cognitive and educational deficits in children born extremely preterm. *Seminars in Perinatology* 32:51–58. [SGF]

Andersson, M. (1994) *Sexual selection*. Princeton University Press. [aMDG]

Andrews, P. A., Gangestad, S. W. & Mathews, D. (2002) Adaptationism – How to carry out an exaptationist program. *Behavioral and Brain Sciences* 25:489–553. [JH]

Archer, J. (1996) Sex differences in social behavior – Are the social role and evolutionary explanations compatible? *American Psychologist* 51(9):909–17. [SGF]

Archer, J. & Mehdikhani, M. (2000) Strategic pluralism: Men and women start from a different point. *Behavioral and Brain Sciences* 23:588. [aMDG]

Arck, P. C., Rose, M., Hertwig, K., Hagen, E., Hildebrandt, M. & Klapp, B.F. (2001) Stress and immune mediators in miscarriage. *Human Reproduction* 16:1505–11. [rMDG]

Arlt, W., Callies, F. & Allolio, B. (2000) DHEA replacement in women with adrenal insufficiency – pharmokinetics, bioconversion, and clinical effects on well-being, sexuality and cognition. *Endocrine Research* 26:505–11. [MVF]

Arnold, F. & Liu, Z. (1986) Sex preference, fertility, and family planning in China. *Population and Development Review* 12:221–46. [NL]

Auchus, R. J. & Rainey, W. E. (2004) Adrenarche – physiology, biochemistry and human disease. *Clinical Endocrinology* 60:288–96. [aMDG]

Aviezer, O., Sagi, A., Resnick, G. & Gini, M. (2002) School competence in young adolescence: Links to early attachment relationships beyond concurrent self-perceived competence and representations of relationships. *International Journal of Behavioral Development* 26:397–409. [aMDG]

Bakermans-Kranenburg, M. J., van IJzendoorn, M. H., Bokhorst, C. L. & Schuengel, C. (2004) The importance of shared environment in infant-father attachment: A behavioral genetic study of the Attachment Q-sort. *Journal of Family Psychology* 18:545–49. [aMDG]

Bakermans-Kranenburg, M. J., van IJzendoorn, M. H. & Juffer, F. (2005) Disorganized infant attachment and preventive interventions: A review and meta-analysis. *Infant Mental Health Journal* 26:191–216. [AJL]

Baldwin, M. W. & Fehr, B. (1995) On the instability of attachment style ratings. *Personal Relationships* 2:247–61. [arMDG]

Barber, N. (2000) On the relationship between country sex ratios and teen pregnancy rates: A replication. *Cross-Cultural Research* 34:26–37. [aMDG]

Barker, D. J. (1998) In utero programming of chronic disease. *Clinical Science* 95:115–28. [MVF]

Barrett, J., Abbott, D. H. & George, L. M. (1990) Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. *Journal of Reproduction and Fertility* 90(2):411–18. [LJS]

Bartholomew, K. (1990) Avoidance of intimacy: An attachment perspective. *Journal of Social and Personal Relationships* 7:147–78. [aMDG]

Bartholomew, K. & Allison, C. J. (2006) An attachment perspective on abusive dynamics in intimate relationships. In: *Dynamics of romantic love: Attachment, caregiving, and sex*, ed. M. Mikulincer & G. S. Goodman, pp. 71–101. Guilford Press. [DKS]

Bartholomew, K. & Horowitz, L. M. (1991) Attachment styles in young adults: A test of a four-category model. *Journal of Personality and Social Psychology* 61:226–44. [arMDG, DKS, VZ]

Bartholomew, K. & Shaver, P. R. (1998) Methods of assessing adult attachment: Do they converge? In: *Attachment theory and close relationships*, ed. J.A. Simpson & W. S. Rholes, pp. 25–45. Guilford Press. [rMDG]

Bateson, P. (2005) The return of the whole organism. *Journal of Biosciences* 30:101–109. [aMDG]

Beijersbergen, M. D., Bakermans-Kranenburg, M. J., Van IJzendoorn, M. H. & Juffer, F. (in press) Stress regulation in adolescents: Physiological reactivity during the adult attachment interview and conflict interaction. *Child Development*. [MJB-K]

Belsky, J. (1997a) Attachment, mating and parenting: An evolutionary interpretation. *Human Nature* 8:361–81. [CDG, aMDG]

(1997b) Variation in susceptibility to environmental influence: An evolutionary argument. *Psychological Inquiry* 8:82–186. [aMDG]

(1999) Modern evolutionary theory and patterns of attachment. In: *Handbook of Attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver, pp. 141–61. Guilford. [CDG, aMDG]

(2000) Fixed versus flexible strategies: Individual differences in facultative responsiveness? *Behavioral and Brain Sciences* 23:591–92. [aMDG]

(2002) Developmental origins of attachment styles. *Attachment and Human Development* 4:166–70. [MVF, aMDG]

(2005) The developmental and evolutionary psychology of intergenerational transmission of attachment. In: *Attachment and bonding: A new synthesis*, ed. C.S. Carter, L. Ahnert, K. E. Grossmann, S. B. Hrdy, M. E. Lamb, S. W. Porges & N. Sachser, pp. 169–98. MIT Press. [aMDG, LP]

(2007) Experience in childhood and the development of reproductive strategies. *Acta Psychologica Scienica* 39:454–68. [DKS]

Belsky, J., Bakermans-Kranenburg, M. J. & van IJzendoorn, M. H. (2007a) For better *and* for worse: Differential susceptibility to environmental influences. *Current Directions in Psychological Science* 16:300–304. [arMDG]

Belsky, J., Steinberg, L. D., Houts, R. M., Friedman, S. L., DeHart, G., Cauffman, E., Roisman, G. I., Halpern-Felsher, B. L., Susman, E. & The NICHD Early Child Care Research Network (2007b) Family rearing antecedents of pubertal timing. *Child Development* 78:1302–21. [aMDG]

Belsky, J., Steinberg, L. & Draper, P. (1991) Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development* 62:647–70. [arMDG, JH, JJJ, DJK, DKS]

Benenson, J. & Christakos, A. (2003) The greater fragility of females' versus males' closest same-sex friendships. *Child Development* 74:1123–29. [CDG]

Benoit, D. & Parker, K. C. H. (1994) Stability and transmission of attachment across three generations. *Child Development* 65:1444–56. [aMDG]

Bereczkei, T. & Csanaky, A. (2001) Stressful family environment, mortality, and child socialisation: Life-history strategies among adolescents and adults from unfavourable social circumstances. *International Journal of Behavioral Development* 25:501–508. [aMDG]

Bernier, A. & Dozier, M. (2002) Assessing adult attachment: Empirical sophistication and conceptual bases. *Attachment and Human Development* 4:171–79. [arMDG]

Bernroider, G., Holztrattner, M. & Rottner, K. (1996) Sex steroid-opioid interactions associated with the temporal component of avian calling patterns. *Hormones and Behavior* 30:583–89. [aMDG]

Betzig, L. (1989) Causes of conjugal dissolution: A cross-cultural study. *Current Anthropology* 30:654–76. [aMDG]

Birnbaum, G. E. (2007) Beyond the borders of reality: Attachment orientations and sexual fantasies. *Personal Relationships* 14:321–42. [arMDG]

Birnbaum, G. E., Reis, H. T., Mikulincer, M., Gillath, O. & Orpaz, A. (2006) When sex is more than just sex: Attachment orientations, sexual experience, and relationship quality. *Journal of Personality and Social Psychology* 91:929–43. [LP, VZ]

Bjorklund, D. F. (1997) The role of immaturity in human development. *Psychological Bulletin* 122:153–69. [aMDG]

Bjorklund, D. F. & Pellegrini, A. D. (2002) *The origins of human nature: Evolutionary developmental psychology*. American Psychological Association Press. [MVF]

Bjorklund, D. F. & Rosenberg, J. S. (2005) The role of developmental plasticity in the evolution of human cognition: evidence from enculturated, juvenile great apes. In: *Origins of the social mind: Evolutionary psychology and child development*, ed. B. J. Ellis & D. F. Bjorklund, pp. 45–75. Guilford Press. [aMDG]

Blurton Jones, N. (1989) The cost of children and the adaptive scheduling of births: Towards a sociobiological perspective on demography. In: *Sociobiology of sexual and reproductive strategies*, ed. A. Rasa, C. Vogel & E. Voland. Chapman and Hall. [aMDG]

Blurton Jones, N. G., Marlowe, F. W., Hawkes, K. & O'Connell, J. F. (2000) Paternal investment and hunter-gatherer divorce rates. In: *Adaptation and human behavior: An anthropological perspective*, ed. L. Cronk, N. Chagnon & W. Irons, pp. 69–90. Aldine De Gruyter. [aMDG]

Bogaert, A. F. & Sadava, S. (2002) Adult attachment and sexual behavior. *Personal Relationships* 9:191–204. [arMDG, VZ]

Bogin, B. (1999) Evolutionary perspective on human growth. *Annual Review of Anthropology* 28:109–53. [MVF, arMDG]

Bokhorst, C. L., Bakermans-Kranenburg, M. J., Fearon, R. M. P., van IJzendoorn, M. H., Fonagy, P. & Schuengel, C. (2003) The importance of shared environment in mother-infant attachment security: A behavioral genetic study. *Child Development* 74:1769–82. [aMDG]

Booth-Laforce, C., Oh, W., Hayoung Kim, A., Rubin, K. H., Rose-.Krasnor, L. & Burgess, K. (2006) Attachment, self-worth, and peer-group functioning in middle childhood. *Attachment and Human Development* 8:309–25. [B-BC, aMDG]

Boothroyd, L. G., Jones, B. C., Burt, D. M., DeBruine, L. M. & Perrett, D. I. (2008) Facial correlates of sociosexuality. *Evolution and Human Behavior* 29:211–18. [LEV]

Borgerhoff Mulder, M. (1989) Menarche, menopause, and reproduction in the Kipsigis of Kenia. *Journal of Biosocial Science* 21:179–92. [aMDG]

(1998) Brothers and sisters: How sibling interactions affect optimal parental allocations. *Human Nature* 9(2):119–62. [RJQ]

Bowlby, J. (1969/1982) *Attachment and loss. Vol. 1. Attachment*, 2nd edition. Basic Books. (Original work published 1969). [CDG, aMDG, DP, DKS, VZ]

(1973) *Attachment and loss. Vol. 2. Separation*. Basic Books. [aMDG]

(1980) *Attachment and loss. Vol. 3. Loss*. Basic Books. [aMDG, NL]

Boyce, W. T. & Ellis, B. J. (2005) Biological sensitivity to context: I. An evolutionary–developmental theory of the origins and functions of stress reactivity. *Development and Psychopathology* 17:271–301. [aMDG]

Brassard, A., Shaver, P. R. & Lussier, Y. (2007) Attachment, sexual experience, and sexual pleasure in romantic relationships: A dyadic approach. *Personal Relationships* 14:475–93. [arMDG, VZ]

Breaugh, J. A. (2003) Effect size estimation: Factors to consider and mistakes to avoid. *Journal of Management* 29:79–97. [rMDG]

Brennan, K. A., Clark, C. L. & Shaver, P. R. (1998) Self-report measurement of adult attachment: An integrative overview. In: *Attachment theory and close relationships*, ed. J.A. Simpson & W. S. Rholes, pp. 46–76. Guilford Press. [arMDG, NL, DKS]

Brennan, K. A. & Shaver, P. R. (1995) Dimensions of adult attachment, affect regulation, and romantic relationship functioning. *Personality and Social Psychology Bulletin* 21:267–83. [VZ]

Bretherton, I. & Munholland, K. A. (1999) Internal working models in attachment relationships: A construct revisited. In: *Handbook of Attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

Bretherton, I., Ridgeway, D. & Cassidy, J. (1990) Assessing internal working models of the attachment relationship: An attachment story completion task. In: *Attachment in the preschool years: Theory, research, and intervention*, ed. M. T. Greenberg, D. Cicchetti, & E. M. Cummings, pp. 273–308. University of Chicago Press. [aMDG, MJB-K]

Brody, S. & Breitenstein, C. (2000) The trade-off between frequency of intercourse and sexual partner accumulation may reflect evolutionary adaptations. *Behavioral and Brain Sciences* 23:594. [rMDG]

Brumbaugh, C. C. & Fraley, R. C. (2006) The evolution of attachment in romantic relationships. In: *Dynamics of romantic love: Attachment, caregiving, and sex*, ed. M. Mikulincer & G. S. Goodman, pp. 71–101. Guilford Press. [DKS]

Brussoni, M. J., Lang, K., Livesley, W. J. & Macbeth, T. M. (2000) Genetic and environmental influences on adult attachment styles. *Personal Relationships* 7:283–89. [aMDG]

Bukowski, W. M., Sippola, L. A. & Newcomb, A. F. (2000) Variations in patterns of attraction to same- and other-sex peers during early adolescence. *Developmental Psychology* 36:147–54. [aMDG]

Bullinaria, J. A. (2007) The effect of learning on life history evolution. In: *Proceedings of the Genetic and Evolutionary Computation Conference (GECCO 2007)*, pp. 222–29. ed. H. Lipson. Association for Computing Machinery. ACM. Available at: http://www.cs.bham.ac.uk/~jxb/PUBS/LELHE.pdf. [DP]

Bureau, J. F., Beliveau, M. J., Moss, E. & Lepine, S. (2006) Association between the mother-child bond and the stories of attachment in the school age. *Canadian Journal of Behavioural Science (Revue Canadienne des Sciences du Comportement)* 38:50–62. [rMDG, MJB-K]

Burnstein, E., Crandall, C. & Kitayama, S. (1994) Some neo-Darwinian decision rules for altruism. *Journal of Personality and Social Psychology* 67:773–89. [JMA]

Buss, D. M. & Greiling, H. (1999) Adaptive individual differences. *Journal of Personality* 67:209–43. [CDG]

Buss, D. M. & Schmitt, D. P. (1993) Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review* 100:204–32. [aMDG]

Butzer, B. & Campbell, L. (2008) Adult attachment, sexual satisfaction, and relationship satisfaction: A study of married couples. *Personal Relationships* 15:141–54. [rMDG, DKS]

Campbell, A. (1992) *The girls in the gang*, 2nd edition. Basil Blackwell. [AC]

(1995) A few good men: The evolutionary psychology of female adolescent aggression. *Ethology and Sociobiology* 16:99–123. [AC]

(1999) Staying alive: Evolution, culture and intrasexual aggression. *Behavioral and Brain Sciences* 22:203–52. [B-BC]

(2000) Putting people before parasites and places. *Behavioral and Brain Sciences* 23:596–97. [aMDG]

(2008a) Attachment, aggression and affiliation: The role of oxytocin in female social behavior. *Biological Psychology* 77:1–10. [rMDG]

(2008b) The morning after the night before: Affective reactions to one-night stands among mated and unmated women and men. *Human Nature* 19:157–73. [AC]

Campbell, B. & Udry, J. R. (1995) Stress and age at menarche of mothers and daughters. *Journal of Biosocial Science* 27:127–34. [aMDG]

Campbell, B. C. (2006) Adrenarche and the evolution of human life history. *American Journal of Human Biology* 18:569–89. [MVF]

Campbell, L., Simpson, J. A., Boldry, J. & Kashy, D. A. (2005) Perceptions of conflict and support in romantic relationships: The role of attachment anxiety. *Journal of Personality and Social Psychology* 88:510–31. [rMDG]

Card, N. A. & Hodges, V. E. (2003) Parent-child relationships and enmity with peers: The role of avoidant and preoccupied attachment. *New Directions for Child and Adolescent Development* 102:23–37. [aMDG]

Carlson, A. A., Ziegler, T. E. & Snowdon C. T. (1997) Ovarian function of pygmy marmoset daughters *(Cebuella pygmaea)* in intact and motherless families. *American Journal of Primatology* 43(4):347–55. [LJS]

Carlson, V., Cicchetti, D., Barnett, D. & Braunwald, K. (1989) Disorganized/disoriented attachment relationships in maltreated infants. *Developmental Psychology* 25:525–31. [aMDG]

Carnelly, K. B. & Brennan, K. A. (2002) Building bridges. *Attachment and Human Development* 4:189–92. [rMDG]

Carter, C. S. (1998) Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology* 23:779–818. [aMDG]

Cashdan, E. (1996) Women's mating strategies. *Evolutionary Anthropology* 5:134–43. [aMDG]

Caspi, A. & Roberts, B. W. (2001) Personality development across the life course: The argument for change and continuity. *Psychological Inquiry* 12:49–66. [JRH]

Cassidy, J. (1988) Child-mother attachment and the self in six-year-olds. *Child Development* 59:121–34. [aMDG, MJB-K]

(1999) The nature of the child's ties. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

(2003) Continuity and change in the measurement of infant attachment: Comment on Fraley and Spieker (2003). *Developmental Psychology* 39:409–12. [aMDG]

Cassidy, J. & Berlin, L. (1994) The insecure/ambivalent pattern of attachment: Theory and research. *Child Development* 65:971–91. [arMDG]

Cassidy, J. & Shaver, P. R., eds. (1999) *Handbook of attachment: Theory, research and clinical applications*. Guilford. [aMDG]

Cellerino, A. & Jannini, E. A. (2005) Male reproductive physiology as a sexually selected handicap? Erectile dysfunction is correlated with general health and health prognosis and may have evolved as a marker of poor phenotypic quality. *Medical Hypotheses* 65:179–84. [SGF]

Cesario S. K. & Hughes, L. A. (2007) Precocious puberty: A comprehensive review of literature. *Journal of Obstetric, Gynecologic, and Neonatal Nursing* 36:263–74. [JRH]

Chan, C., Eric, B. & Chan C. (2006) Attitudes to and practices regarding sex selection in China. *Prenatal Diagnosis* 26:610–13. [NL]

Chang, F., Kidd, J. R., Livak, K. J., Pakstis, A. J. & Kidd, K. K. (1996) The world-wide distribution of allele frequencies at the human dopamine D4 receptor locus. *Human Genetics* 98:91–101. [rMDG]

Chasiotis, A., Scheffer, D., Restemeier, R. & Keller, H. (1998) Intergenerational context discontinuity affects the onset of puberty: A comparison of parent–child dyads in West and East Germany. *Human Nature* 9:321–39. [aMDG]

Chen, C. C. G. & Parker, C. R. Jr. (2004) Adrenal androgens and the immune system. *Seminars in Reproductive Medicine* 22:369–77. [MVF]

Chisholm, J. S. (1993) Death, hope, and sex: Life-history theory and the development of reproductive strategies. *Current Anthropology* 34:1–24. [aMDG, JH]

(1996) The evolutionary ecology of attachment organization. *Human Nature* 7:1–38. [aMDG, JH, RJQ]

(1999) *Death, hope and sex: Steps to an evolutionary ecology of mind and morality*. Cambridge University Press. [arMDG, JH, DKS]

Chisholm, J. S., Burbank, V. K., Coall, D. A. & Gemmiti, F. (2005a) Early stress: Perspectives from developmental evolutionary ecology. In: *Origins of the social mind: Evolutionary psychology and child development*, ed. B.J. Ellis & D. F. Bjorklund, pp. 76–107. Guilford. [aMDG]

Chisholm, J. S., Quinlivan, J. A., Petersen, R. W. & Coall, D. A. (2005b) Early stress predicts age at menarche and first birth, adult attachment, and expected lifespan. *Human Nature* 16:233–65. [aMDG]

Cho, J., Holditch-Davis, D. & Belyea, M. (2007) Gender and racial differences in the looking and talking behaviors of mothers and their 3-year-old prematurely born children. *Journal of Pediatric Nursing* 22(5):356–67. [SGF]

Chugani, H. T. (1998) Critical period of brain development: Studies of cerebral glucose utilization with PET. *Preventive Medicine* 27:184–88. [MVF]

Clark, A. & Daly, M. (2005) What is the significance of cross-national variability in sociosexuality? *Behavioral and Brain Sciences* 28:280. [aMDG]

Clutton-Brock, T. H. (1991) *The evolution of parental care*. Princeton University Press. [aMDG, NL, RJQ]

(2002) Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72. [aMDG]

Clutton-Brock, T. H., ed. (1988) *Reproductive success: Studies of individual variation in contrasting breeding systems*. The University of Chicago Press. [DM]

Coale, A. J. & Banister, J. (1996) Five decades of missing females in China. *Proceedings of the American Philosophical Society* 140:421–50. [rMDG]

Cohen, D. L. & Belsky, J. (2008) Individual differences in female mate preferences as a function of attachment and hypothetical ecological conditions. *Journal of Evolutionary Psychology* 6:25–42. [rMDG]

Cohen, J. (1988) *Statistical power analysis for the behavioral sciences*. Erlbaum. [rMDG]

Collins, N. L. & Read, S. J. (1990) Adult attachment, working models and relationship quality in dating couples. *Journal of Personality and Social Psychology* 58:644–63. [aMDG]

Comings, D. E., Muhlemann, D., Johnson, J. P. & Mac Murray, J. P. (2002) Parent-daughter transmission of the androgen receptor gene as an explanation of the effect of father absence on age of menarche. *Child Development* 73:1046–51. [aMDG]

Compagnone, N. A. & Mellon, S. H. (1998) Dehydroepiandrosterone: A potential signaling molecule for neocortical organization during development. *Proceedings of the National Academy of Sciences USA* 95:4678–83. [MVF]

Cooper, E. (2006) *The runaway and homeless youth program: Administrative, funding, and legislative action.* Congressional Research Service, Library of Congress. Available at: http://digital.library.unt.edu/govdocs/crs/permalink/meta-crs-9962:1. [MJK]

Cooper, M. L., Shaver, P. R. & Collins, N. L. (1998) Attachment styles, emotion regulation, and adjustment in adolescence. *Journal of Personality and Social Psychology* 74:1380–97. [arMDG]

Corby, B. C. (2006) Attachment and adjustment in preadolescence. Unpublished doctoral dissertation, Psychology Department, Florida Atlantic University. [arMDG]

Cosmides, L. & Tooby, J. (1994) Origins of domain specificity: The evolution of functional organization. In: *Mapping the mind: Domain specificity in cognition and culture*, ed. L. A. Hirschfeld & S. A. Gelman, pp. 85–116. Cambridge University Press. [DJK]

Costa, R. M. & Brody, S. (2007) Women's relationship quality is associated with specifically penile-vaginal intercourse orgasm and frequency. *Journal of Sex and Marital Therapy* 33:319–27. [rMDG]

Cramer, K. M. & Neyedley, K. A. (1998) Sex differences in loneliness: The role of masculinity and femininity. *Sex Roles* 38:645–50. [VZ]

Crawford, C. & Anderson, J. (1989) Sociobiology: An environmentalist discipline? *American Psychologist* 44:1449–60. [DJK]

Crawford, T. N., Shaver, P. R., Cohen, P., Pilkonis, P. A., Gillath, O. & Kasen, S. (2006) Self-reported attachment, interpersonal aggression, and personality disorder in a prospective community sample of adolescents and adults. *Journal of Personality Disorders* 20:331–51. [rMDG]

Critchfield, K. L., Levy, K. N., Clarkin, J. F. & Kernberg, O. F. (2008) The relational context of aggression in Borderline Personality Disorder: Using adult attachment style to predict forms of hostility. *Journal of Clinical Psychology* 64:67–82. [AC]

Cronin, H. (1991) *The ant and the peacock*. Cambridge University Press. [LB]

Cronk, L. (2000) Female-biased parental investment and growth performance among the Mukogodo. In: *Adaptation and human behavior: An anthropological perspective*, ed. L. Cronk, N. Chagnon, & W. Irons, pp. 203–21. [RJQ]

Crowell, J. A., Fraley, R. C. & Shaver, P. R. (1999/2008) Measurement of individual differences in adolescent and adult attachment. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford (2nd Edition). [LB, aMDG]

Crowell, J. A., Treboux, D. & Waters, E. (2002) Stability of attachment representations: The transition to marriage. *Developmental Psychology* 38:467–79. [aMDG]

Cummings, F. M. (2003) Toward assessing attachment on an emotional security continuum: Comment on Fraley and Spieker (2003). *Developmental Psychology* 39:405–408. [aMDG]

Cushing, B. S. & Kramer, K. M. (2005) Mechanisms underlying epigenetic effects of early social experience: The role of neuropeptides and steroids. *Neuroscience and Biobehavioral Reviews* 29:1089–105. [B-BC]

Daly, M. & Wilson, M. (1996) Violence against stepchildren. *Current Directions in Psychological Science* 5:77–81. [rMDG]

David, D. H. & Lyons-Ruth, K. (2005) Differential attachment responses of male and female infants to frightening maternal behavior: Tend or befriend versus fight or flight? *Infant Mental Health Journal* 26:1–18. [aMDG]

Davies, P. T. & Forman, E. M. (2002) Children's patterns of preserving emotional security in the interparental subsystem. *Child Development* 73:1880–903. [B-BC]

Davis, D., Shaver, P. R. & Vernon, M. L. (2004) Attachment style and subjective motivations for sex. *Personality and Social Psychology Bulletin* 30:1076–90. [DKS]

Davis, M. & Emory, E. (1995) Sex differences in neonatal stress reactivity. *Child Development* 66:14–27. [SGF]

Dawkins, R. (2006) *The selfish gene.* Oxford University Press. [JMA]

DeKlyen, M., Speltz, M. & Greenberg, M. T. (1999) Fathering and early onset conduct problems: Positive and negative parenting, father–son attachment, and the marital context. *Clinical Child and Family Psychology Review* 1:3–21. [aMDG]

Del Giudice, M. (2008) Sex-biased ratio of avoidant/ambivalent attachment in middle childhood. *British Journal of Developmental Psychology*. 26:369–79. [aMDG, MJB-K]

Del Giudice, M., Angeleri, R. & Manera, V. (in press) The juvenile transition: A developmental switch point in human life history. *Developmental Review*. doi:10.1016/j.dr.2008.09.001 [rMDG]

Delton, A. W., Robertson, T. E. & Kenrick, D. T. (2006) The mating game isn't over: A reply to Buller's critique of the evolutionary psychology of mating. *Evolutionary Psychology* 4:262–73. [aMDG]

Deulofeut, R., Dudell, G. & Sola, A. (2007) Treatment-by-gender effect when aiming to avoid hyperoxia in preterm infants in the NICU. *Acta Paediatrica* 96:990–94. [SGF]

De Wolff, M.S. & van IJzendoorn, M. H. (1997) Sensitivity and attachment: A meta-analysis on parental antecedents of infant attachment. *Child Development* 68:571–91. [JH, AJL]

Dhom, G. (1973) The prepubertal and pubertal growth of the adrenal (adrenarche). *Beitrage Pathologie* 150:357–77. [MVF]

Ding, Q. J. & Hesketh, T. (2006) Family size, fertility preferences, and sex ratio in China in the era of the one child family policy: Results from national family planning and reproductive health survey. *British Medical Journal* 333:371–73. [rMDG]

Ding, Y. C., Chi, H. C., Grady, D. L., Morishima, A., Kidd, J. R., Kidd, K. K., Foldman, P., Spence, M. A., Schuck, S., Swanson, J. M., Zhang, Y. P. & Moyzis, R. K. (2002) Evidence of positive selection at the human dopamine receptor D4 gene locus. *Proceedings of the National Academy of Sciences USA* 99:309–14. [rMDG]

Dishion, T. J., Duncan, T. E., Eddy, J. M., Fagot, B. I. & Fetrow, R. (1994) The world of parents and peers: Coercive exchanges and children's social adaptation. *Social Development* 3:255–68. [JRH]

Doligez, B., Danchin, E. & Clobert, J. (2002) Public information and breeding habitat selection in a wild bird population. *Science* 297:1168–70. [JRH]

Domes, G., Heinrichs, M., Michel, A., Berger, C. & Herpetz, S. C. (2007) Oxytocin improves "mind-reading" in humans. *Biological Psychiatry* 61:731–33. [rMDG]

Dong, M. & Li, S. (2007) Conflict resolution in Chinese family purchase decisions: The impact of changing female roles and marriage duration. *International Journal of Conflict Management* 18:308–24. [NL]

D'Onofrio, B. M., Turkheimer, E., Emery, R. E., Slutske, W. S., Heath, A. C., Madden, P. A. & Martin, N. G. (2006) A genetically informed study of the processes underlying the association between parental marital instability and offspring adjustment. *Developmental Psychology* 42:486–99. [rMDG]

Doran, J. E. (1994) Modelling early human societies. *Artificial Intelligence and Simulation of Behaviour Quarterly* 90(5):31–33. Available at: http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.55.2287. [DP]

Draper, P. (1989) African marriage systems: Perspectives from evolutionary ecology. *Ethology and Sociobiology* 10:145–69. [aMDG]

Draper, P. & Harpending, H. (1982) Father absence and reproductive strategy: An evolutionary perspective. *Journal of Anthropological Research* 38:255–73. [MVF, aMDG]

(1988) A sociobiological perspective on the development of human reproductive strategies. In: *Sociobiological perspectives on human development*, ed. K. B. MacDonald, pp. 340–72. Springer-Verlag. [aMDG]

Ducharme, J., Doyle, A. B. & Markiewicz, D. (2002) Attachment security with mother and father: Associations with adolescents' reports of interpersonal behavior with parents and peers. *Journal of Social and Personal Relationships* 19:203–31. [aMDG]

Dunbar, R. I. M. & Schultz, S. (2007) Evolution in the social brain. *Science* 317:1344–47. [aMDG]

Durrett, M. E., Otaki, M. & Richards, P. (1984) Attachment and the mother's perception of support from the father. *International Journal of Behavioral Development* 7:167–76. [NL]

Easterbrooks, A., Biesecker, G. & Lyons-Ruth, K. (2000) Infancy predictors of emotional availability in middle childhood: The role of attachment security and maternal depressive symptomatology. *Attachment and Human Development* 2(2):170–87. [MJK]

Egan, V. & Angus, S. (2004) Is social dominance a sex-specific strategy for infidelity? *Personality and Individual Differences* 36:575–86. [aMDG]

Eibl-Eibesfeldt, I. (1989) *Human ethology*. Aldine de Gruyter. [aMDG]

Ellis, B. J. (1998) The Partner-Specific Investment Inventory: An evolutionary approach to individual differences in investment. *Journal of Personality* 66:383–441. [rMDG]

(2004) Timing of pubertal maturation in girls: An integrated life history approach. *Psychological Bulletin* 130:920–58. [arMDG, JJJ. LP]

(2005) Determinants of pubertal timing: An evolutionary developmental approach. In: *Origins of the social mind: Evolutionary psychology and child development*, ed. B.J. Ellis & D. F. Bjorklund, pp. 164–88. Guilford. [aMDG]

Ellis, B. J. & Essex, M. J. (2007) Family environments, adrenarche, and sexual maturation: A longitudinal test of a life history model. *Child Development* 78:1799–817. [MVF, arMDG]

Ellis, B. J. & Garber, J. (2000) Psychosocial antecedents of variation in girls' pubertal timing: Maternal depression, stepfather presence, and marital and family stress. *Child Development* 71:485–501. [JJJ]

Ellis, B. J., Jackson, J. J. & Boyce, W. T. (2006) The stress response system: Universality and adaptive individual differences. *Developmental Review* 26:175–212. [aMDG]

Ellison, P. T. (2001) *On fertile ground: A natural history of human reproduction*. Harvard University Press. [arMDG]

Emery, J., Paguette, D. & Bigras, M. (2008) Factors predicting attachment patterns in infants of adolescent mothers. *Journal of Family Studies* 14:65–90. [NL]

Emlen, D. (1997) Alternative reproductive tactics and male dimorphism in the horned beetle *Onthophagus acuminatus (Coleoptera: Scarabaeidae)*. *Behavioral Ecology and Sociobiology* 41:335–41. [aMDG]

Erickson, M. F., Sroufe, L. A. & Egeland, B. (1985) The relationship between quality of attachment and behavior problems in preschool in a high-risk sample. *Monographs of the Society for Research in Child Development* 50:147–66. [aMDG]

Feeney, B. C. & Collins, N. L. (2001) Predictors of caregiving in adult intimate relationships: An attachment theoretical perspective. *Journal of Personality and Social Psychology* 80:972–94. [VZ]

Feeney, J. A. (1999) Adult romantic attachment and couple relationships. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver, pp. 355–77. Guilford Press. [B-BC, aMDG, LP]

(2002) Attachment-related dynamics: What can we learn from self-reports of avoidance and anxiety? *Attachment and Human Development* 4:193–200. [rMDG]

Feeney, J. A. & Noller, P. (1990) Attachment style as a predictor of adult romantic relationships. *Journal of Personality and Social Psychology* 58:281–91. [aMDG]

(2004) Attachment and sexuality in close relationships. In: *Handbook of sexuality in close relationships*, ed. J. H. Harvey, A. Wenzel, and S. Sprecher, pp. 183–201. Erlbaum. [DKS]

Feeney, J. A., Noller, P. & Patty, J. (1993) Adolescents' interactions with the opposite sex: Influence of attachment style and gender. *Journal of Adolescence* 16:169–89. [DKS]

Feinberg, D. R., Jones, B. C., Law-Smith, M. J., Moore, F. R., DeBruine, L. M., Cornwell, R. E., Hillier, S. G. & Perrett, D. I. (2006) Menstrual cycle, trait estrogen level, and masculinity preferences in the human voice. *Hormones and Behavior* 49:215–22. [LEV]

Figueredo, A. J. & Jacobs, W. J. (2000) Strategic pluralism through a Brunswikian lens. *Behavioral and Brain Sciences* 23:603–604. [JJJ]

Figueredo, A. J., Vásquez, G., Brumbach, B. H. & Schneider, S. M. R. (2004) The heritability of life history strategy: The K-factor, covitality, and personality. *Social Biology* 51:121–43. [AJF, arMDG]

(2007) The K-factor, covitality, and personality: A psychometric test of life history theory. *Human Nature* 18(1):47–73. [AJF]

Figueredo, A. J., Vásquez, G., Brumbach, B., Schneider, S. M. R., Sefcek, J. A., Tal, I. R., Hill, D., Wenner, C. J. & Jacobs, W. J. (2006) Consilience and life history theory: From genes to brain to reproductive strategy. *Developmental Review* 26:243–75. [AJF, aMDG]

Finkel, D., Wille, D. E. & Matheny, A. P. (1998) Preliminary results from a twin study of infant-caregiver attachment. *Behavior Genetics* 28:1–8. [aMDG]

Finnegan, R. A., Hodges, E. & Perry, D. (1996) Preoccupied and avoidant coping during middle childhood. *Child Development* 67:1318–28. [B-BC, arMDG]

Flinn, M. V. (2006) Evolution and ontogeny of stress response to social challenges in the human child. *Developmental Review* 26:138–74. [MVF, rMDG]

Flinn, M. V., Geary, D. C. & Ward, C. V. (2005) Ecological dominance, social competition, and coalitionary arms races: Why humans evolved extraordinary intelligence. *Evolution and Human Behavior* 26(1):10–46. [MVF]

Flinn, M. V. & Ward, C. V. (2005) Ontogeny and evolution of the social child. In: *Origins of the social mind: Evolutionary psychology and child development*, ed. B. J. Ellis & D. F. Bjorklund, pp. 19–44. Guilford Press. [aMDG]

Fortuna, K. & Roisman, G. I. (2008) Insecurity, stress, and symptoms of psychopathology: Contrasting results from self-reports versus interviews of adult attachment. *Attachment and Human Development* 10:11–28. [rMDG]

Fraley, R., Brumbaugh, C. C. & Marks, M. J. (2005) The evolution and function of adult attachment: A comparative and phylogenetic analysis. *Journal of Personality and Social Psychology* 89:731–46. [LP]

Fraley, R. C. (2002) Attachment stability from infancy to adulthood: Meta-analysis and dynamic modeling of developmental mechanisms. *Personality and Social Psychology Review* 6:123–51. [aMDG]

Fraley, R. C. & Shaver, P. R. (1997) Adult attachment and the suppression of unwanted thoughts. *Journal of Personality and Social Psychology* 73:1080–91. [VZ]

Fraley, R. C. & Spieker, S. J. (2003) Are infant attachment patterns continuously or categorically distributed? A taxometric analysis of Strange Situation behavior. *Developmental Psychology* 39:387–404. [aMDG, NL]

Fraley, R. C., Waller, N. G. & Brennan, K. A. (2000) An item response theory analysis of self-report measures of adult attachment. *Journal of Personality and Social Psychology* 78:350–65. [rMDG]

Francis, D. D., Young, L. J., Meaney, M. J. & Insel, T. R. (2002) Naturally occurring differences in maternal care are associated with the expression of oxytocin and vasopressin (V1a) receptors: Gender differences. *Journal of Neuroendocrinology* 14:349–53. [B-BC, SGF]

Frisch, R. E. (1988) Fatness and fertility. *Scientific American* 258(3):88–95. [JRH]

Furstenberg, F. F. & Nord, C. W. (1985) Parenting apart: Patterns of childrearing after marital disruption. *Journal of Marriage and the Family* 47:893–904. [aMDG]

Furstenberg, F. F., Peterson, J. L., Nord, C. W. & Zill, N. (1983) The life course of children of divorce: Marital disruption and marital contact. *American Sociological Review* 48:656–68. [aMDG]

Gangestad, S. W. & Simpson, J. A. (1990) Towards an evolutionary history of female sociosexual variation. *Journal of Personality* 58:69–96. [LB, aMDG]

(2000) The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences* 23:573–87; discussion 597–644. [aMDG, JH, JJJ, LP. LEV]

Gangestad, S. W. & Thornhill, R. (1997) The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior* 18:69–88. [VZ]

(2008) Human oestrus. *Proceedings of the Royal Society B (Biological Sciences)* 275:991–1000. [LEV]

Geary, D. C. (1998) *Male, female. The evolution of human sex differences*. American Psychological Association. [aMDG]

(2000) Evolution and proximal expression of human paternal investment. *Psychological Bulletin* 126:55–77. [aMDG]

(2002) Sexual selection and human life history. *Advances in Child Development and Behavior* 30:41–101. [aMDG]

(2005a) Evolution of paternal investment. In: *The evolutionary psychology handbook*, ed. D. M. Buss, pp. 483–505. Wiley & Sons. [aMDG]

(2005b) *The origin of mind.* American Psychological Association. [MVF]

Geary, D. C. & Bjorklund, D. F. (2000) Evolutionary developmental psychology. *Child Development* 71:57–65. [MVF, aMDG]

Geary, D. C. & Flinn, M. V. (2001) Evolution of human parental behavior and the human family. *Parenting: Science and Practice* 1:5–61. [aMDG]

(2002) Sex differences in behavioral and hormonal response to social threat. *Psychological Review* 109(4):745–50. [MVF]

Gentzler, A. L. & Kerns, K. A. (2004) Associations between insecure attachment and sexual experiences. *Personal relationships* 11:249–65. [B-BC, arMDG]

George, C. & West, M. (1999) Developmental vs. social personality models of adult attachment and mental ill health. *British Journal of Medical Psychology* 72:285–303. [aMDG]

Gilissen, R., Bakermans-Kranenburg, M. J., Van IJzendoorn, M. H. & Linting, M. (2008) Electrodermal reactivity during the Trier Social Stress Test for Children: Interaction between the serotonin transporter polymorphism and children's attachment representation. *Developmental Psychobiology* 50(6):615–25. [rMDG, MJB-K]

Gimpl, G. & Fahrenholz, F. (2001) The oxytocin receptor system: Structure, function and regulation. *Physiological Reviews* 81:629–83. [rMDG]

Gloger-Tippelt, G. & Konig, L. (2007) Attachment representations in 6-year-old children from one and two parent families in Germany. *School Psychology International* 28:313–30. [rMDG, MJB-K]

Gluckman, P. D. & Hanson, M. A. (2006) Evolution, development and timing of puberty. *Trends in Endocrinology and Metabolism* 17:7–12. [MVF]

Godbout, N., Lussier, Y. & Sabourin, S. (2006) Early abuse experiences and subsequent gender differences in couple adjustment. *Violence and Victims* 21:744–60. [rMDG]

Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., Nugent, T. F., Herman, D. H., Clasen, L. S., Toga, A. W., Rapoport, J. L. & Thompson, P. M. (2004) Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences USA* 101:817–19. [MVF]

Goldenson, J., Geffner, R., Foster, S. L. & Clipson, C. R. (2007) Female domestic violence offenders: Their attachment security, trauma symptoms, and personality organization. *Violence and Victims* 22:532–45. [AC, rMDG]

Goldstein Ferber, S. (2008) The concept of co-regulation between neurobehavioral sub-systems: The logic interplay between excitatory and inhibitory ends. *Behavioral and Brain Sciences* 31(3):337–38. [SGF]

Gottesmann, I. I. (1966) Genetic variance in an adaptive personality trait. *Journal of Child Psychology and Psychiatry* 7:199–208. [aMDG]

Graham, C. A. & Easterbrooks, M. A. (2000) School-aged children's vulnerability to depressive symptomatology: The role of attachment security, maternal depressive symptomatology, and economic risk. *Development and Psychopathology* 12:201–13. [KAK]

Granot, D. & Mayseless, O. (2001) Attachment security and adjustment to school in middle childhood. *International Journal of Behavioral Development* 25:530–41. [B-BC, arMDG, MJB-K]

Green, J., Stanley, C., Smith, V. & Goldwyn, R. (2000) A new method of evaluating attachment representations in school-age children: The Manchester Child Attachment Story Task. *Attachment and Human Development* 2:48–70. [aMDG]

Green, J. M. & Goldwyn, R. (2002) Attachment disorganization and psychopathology: New findings in attachment research and their potential implications for developmental psychopathology in childhood. *Journal of Child Psychology and Psychiatry* 43:835–46. [AJL]

Greenberg, M. T. (1999) Attachment and psychopathology in childhood. In: *Handbook of Attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

Gross, M. R. (1996) Alternative reproductive strategies and tactics: Diversity within sexes. *Trends in Ecology and Evolution* 11:92–98. [aMDG, JJJ]

Grossmann, K. E., Grossmann, K. & Waters, E., eds. (2005) *Attachment from infancy to adulthood: The major longitudinal studies.* Guilford Press. [aMDG]

Grossmann, K. E., Grossmann, K. & Zimmermann, P. (1999) A wider view of attachment and exploration: stability and change during the years of immaturity. In: *Handbook of Attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

Guastella, A. J., Mitchell, P. B. & Dadds, M. R. (2008) Oxytocin increases gaze to the eye region of human faces. *Biological Psychiatry* 63:3–5. [rMDG]

Gurven, M. & Walker, R. (2006) Energetic demand of multiple dependents and the evolution of slow human growth. *Proceedings of the Royal Society of London B* 273:835–41. [aMDG]

Guttmann-Steinmetz, S. & Crowell, J. A. (2006) Attachment and externalizing disorders: A developmental psychopathology perspective. *Journal of the American Academy of Child and Adolescent Psychiatry* 45:440–51. [B-BC]

Hagen, E. H. & Hammerstein, P. (2005) Evolutionary biology and the strategic view of ontogeny: Genetic strategies provide robustness and flexibility in the life course. *Research in Human Development* 2:87–101. [aMDG]

Hamilton, C. E. (2000) Continuity and discontinuity of attachment from infancy through adolescence. *Child Development* 71:690–94. [aMDG]

Hamilton, W. D. (1964) The genetical evolution of social behaviour, Parts I and II. *Journal of Theoretical Biology* 7:1–52. [aMDG, LJS]

Handcock, M. S. & Morris, M. (1999) *Relative distribution methods in the social sciences*. Springer-Verlag. [rMDG]

Harel, J. & Scher, A. (2003) Insufficient responsiveness in ambivalent mother-infant relationships: Contextual and affective aspects. *Infant Behavior and Development* 26:371–83. [aMDG]

Harlow, H. & Harlow, M. K. (1965) The affectional systems. In: *Behavior of nonhuman primates, vol. 2*, ed. A. M. Schrier, H. F. Harlow & F. Stollnitz, pp. 287–334. Academic Press. [VZ]

Harlow, H. F. (1964) Early social deprivation and later behavior in the monkey. In: *Unfinished tasks in the behavioral sciences*, ed. A. Abrams, H. H. Gurner, & J. E. P. Tomal, pp. 154–73. Williams & Wilkins. [DJK]

Harpending, H. & Cochran, G. (2002) In our genes. *Proceedings of the National Academy of Sciences USA* 99:10–12. [rMDG, LP]

Harris, J. R. (1995) Where is the child's environment? A group socialization theory of development. *Psychological Review* 102:458–89. [aMDG]

(1998) *The nurture assumption*. Free Press. [JRH]

(2005) Social behavior and personality development. In: *Origins of the social mind: Evolutionary psychology and child development*, ed. B. J. Ellis & D. F. Bjorklund, pp. 245–70. Guilford. [aMDG]

(2006) *No two alike: Human nature and human individuality*. Norton. [JRH]

Hawley, P. H. (2007) Social dominance in childhood and adolescence: Why social competence and aggression may go hand in hand. In: *Aggression and adaptation: The bright side to bad behavior*, ed. P. H. Hawley, T. D. Little & P. C. Rodkin, pp. 1–29. Erlbaum. [B-BC]

Hazan, C., Campa, M. & Gur-Yaish, N. (2006) What is adult attachment? In: *Dynamics of romantic love: Attachment, caregiving, and sex*, ed. M. Mikulincer & G. S. Goodman, pp. 47–70. Guilford Press. [DKS]

Hazan, C. & Diamond, L. (2000) The place of attachment in human mating. *Review of General Psychology* 4:186–204. [VZ]

Hazan, C. & Shaver, P. R. (1987) Romantic love conceptualized as an attachment process. *Journal of Personality and Social Psychology* 52:511–24. [aMDG, DKS, VZ]

Hazan, C. & Zeifman, D. (1999) Pair bonds as attachments: Evaluating the evidence. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford Press. [aMDG]

Heath, K. & Hadley, C. (1998) Dichotomous male reproductive strategies in a polygynous human society: Mating versus parental effort. *Current Anthropology* 39:369–74. [DJK]

Heckmann, M., Hartmann, F. M., Kampschulte, B., Gack, H., Bodeker, R. H., Gorther, L. & Wudy, S. A. (2005) Cortisol production rates in preterm infants in relation to growth and illness: A noninvasive prospective study using gas chromatography-mass spectrometry. *Journal of Clinical Endocrinology and Metabolism* 90(10):5737–42. [SGF]

Henderson, A. J. Z., Bartholomew, K. & Dutton, D. G. (1997) He loves me, he loves me not: Attachment and separation resolution of abused women. *Journal of Family Violence* 12:169–91. [aMDG]

Hennebert, O., Chalbot, S., Alran, S. & Morfin, R. (2007) Dehydroepiandrosterone 7alpha-hydroxylation in human tissues: Possible interference with type 1 11beta-hydroxysteroid dehydrogenase-mediated processes. *Journal of Steroid Biochemistry and Molecular Biology* 104:326–33. [MVF]

Herdt, G. & McClintock, M. (2000) The magical age of 10. *Archives of Sexual Behavior* 29:587–606. [aMDG]

Hesse, E. (1999) The Adult Attachment Interview: Historical and current perspectives. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG, MJB-K]

Hesse, E. & Main, M. (2000) Disorganized infant, child, and adult attachment: Collapse in behavioral and attentional strategies. *Journal of the American Psychoanalytic Association* 48:1097–1127. [AJL]

(2006) Frightening, threatening, and dissociative parental behavior in low-risk samples: Description, discussion, and interpretations. *Development and Psychopathology* 18:309–43. [aMDG]

Hewlett, B. S., Lamb, M. E., Leyendecker, B. & Schölmerich, A. (2000) Parental investment strategies among Aka foragers, Ngandu farmers, and Euro American urban-industrialists. In: *Adaptation and human behavior: An anthropological perspective*, ed. L. Cronk, N. Chagnon & W. Irons, pp. 155–78. Aldine De Gruyter. [aMDG]

Hill, K. (1993) Life history theory and evolutionary anthropology. *Evolutionary Anthropology* 2:78–88. [aMDG]

Hill, K. & Hurtado, A. M. (1996) *Ache life history: The ecology and demography of a foraging people*. Aldine De Gruyter. [aMDG]

Hill, K. & Kaplan, K. (1988) Tradeoffs in male and female reproductive strategies among the Ache. In: *Human reproductive behavior: A Darwinian perspective*, ed. L. Betzig, M. Borgerhoff Mulder & P. Turke. Cambridge University Press. [aMDG]

Hinde, R. A. (1982) Attachment: Some conceptual and biological issues. In: *The place of attachment in human behavior*, ed. C.M. Parkes & J. Stevenson-Hinde, pp. 60–76. Basic Books. [aMDG]

Hofer, M. A. (1994) Early relationships as regulators of infant physiology and behavior. *Acta Paediatrica* (Suppl.) 397:9–18. [SGF]

Höglund, J. & Sheldon, B. C. (1998) The cost of reproduction and sexual selection. *Oikos* 83:478–83. [aMDG]

Hoier, S. (2003) Father absence and age at menarche: A test of four evolutionary models. *Human Nature* 14:209–33. [CDG, LP]

Hollander, J. (2008) Testing the grain-size model for the evolution of phenotypic plasticity. *Evolution* 62:1381–89. [LP]

Holtzworth-Munroe, A. & Stuart, G. (1994) Typologies of male batterers: Three subtypes and the differences among them. *Psychological Bulletin* 116:476–97. [AC]

Hönekopp, J., Rudolph, U., Beier, L., Liebert, A. & Müller, C. (2007) Physical attractiveness of face and body as indicators of physical fitness. *Evolution and Human Behavior* 28:106–11. [JH]

House, J. S., Landis, K. R. & Umberson, D. (1988) Social relationships and health. *Science* 241:540–45. [VZ]

Houston, A. I. & McNamara, J. M. (1999) *Models of adaptive behaviour. An approach based on state*. Cambridge University Press. [arMDG]

Hrdy, S. B. (1981) *The woman that never evolved*. Harvard University Press. [B-BC]

(1999) *Mother nature*. Pantheon Books. [arMDG]

(2000) The optimal number of fathers: evolution, demography, and history in the shaping of female mate preferences. *Annals of the New York Academy of Sciences* 907:75–96. [aMDG]

(2005a) Comes the child before the man: Cooperative breeding and the evolution of prolonged post-weaning dependence. In: *Hunter gatherer childhoods: Evolutionary, developmental and cultural perspectives*, ed. B. Hewlett & M. Lamb. Aldine/Transaction. [aMDG]

(2005b) Evolutionary context of human development: The cooperative breeding model. In: *Attachment and bonding: A new synthesis*, ed. C. S. Carter, L. Ahnert, K. E. Grossmann, S. B. Hrdy, M. E. Lamb, S.W. Porges & N. Sachser, pp. 9–32. MIT Press. [aMDG]

Hu, P. & Meng, Z. (2003) Research on discrimination of mother-infant attachment type. *Acta Psychologica Sinica* 35:201–208. [NL]

Huber, D., Veinante, P. & Stoop, R. (2005) Vasopressinand oxytocin excite distinct neuronal populations in the central amygdala. *Science* 308:245–48. [SGF]

Hyde, J. S. (2005) The gender similarities hypothesis. *American Psychologist* 60:581–92. [LP]

Ibáñez, L., Dimartino-Nardi, J., Potau, N. & Saenger, P. (2000) Premature adrenarche – normal variant or forerunner of adult disease. *Endocrine Reviews* 21:671–96. [aMDG]

Impett, E. A. & Peplau, L. A. (2002) Why some women consent to unwanted sex with a dating partner: Insights from attachment theory. *Psychology of Women Quarterly* 26:360–70. [aMDG]

Ingemarsson, I. (2003) Gender aspects of preterm birth. *British Journal of Obstetrics and Gynaecology* 110(20):34–38. [SGF]

Insel, T. R. (2000) Toward a neurobiology of attachment. *Review of General Psychology* 4:176–85. [aMDG]

Insel, T. R. & Young, L. J. (2001) The neurobiology of attachment. *Nature Neuroscience* 2:129–36. [aMDG]

Jackson, J. J. & Ellis, B. J. (submitted) The development of human reproductive strategies: toward a comprehensive model. [JJJ]

Jackson, J. J., Ellis, B. J. & Garber, J. (submitted) Sex differences in the developmental antecedents of life history strategies: Tests of an integrated theory. [JJJ]

Jackson, J. J. & Kirkpatrick, L. A. (2007) The structure and measurement of human mating strategies: Towards a multidimensional model of sociosexuality. *Evolution and Human Behavior* 28:382–91. [arMDG, LP]

Jang, S. A., Smith, S. W. & Levine, T. R. (2002) To stay or to leave? The role of attachment styles in communication patterns and potential termination of romantic relationships following discovery of deception. *Communication Monographs* 69:236–52. [aMDG]

Jezova, D., Jurankova, E., Mosnarova, A., Kriska, M. & Skultetyova, I. (1996) Neuroendocrine response during stress with relation to gender differences. *Acta Neurobiologae Experimentalis* 56:779–85. [aMDG]

Jones, H. P., Karuri, S., Cronin, C. M. G., Ohlsson, A., Peliowski, A., Synnes, A., Lee, S. K. & the Canadian Neonatal Network (2005) Actuarial survival of a large Canadian cohort of preterm infants. *BMC Pediatrics* 5:40. [SGF]

Jorm, A. F., Christensen, H., Rodgers, B., Jacomb, P. A. & Easteal, S. (2004) Association of adverse childhood experiences, age of menarche, and adult reproductive behavior: Does the androgen receptor gene play a role? *American Journal of Medical Genetics, B* 125:105–11. [aMDG]

Juvonen, J., Graham, S. & Schuster, M. A. (2003) Bullying among young adolescents: The strong, the weak, and the troubled. *Pediatrics* 112:1231–37. [aMDG]

Kanazawa, S. (2001) Why father absence might precipitate early menarche: The role of polygyny. *Evolution and Human Behavior* 22:329–34. [aMDG]

Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. (2000) A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology* 9:156–85. [aMDG]

Kaplan, H. & Robson, A.J. (2002) The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proceedings of the National Academy of Sciences* 99:10221–226. [aMDG]

Kaplan, H. S. & Gangestad, S. W. (2005) Life history theory and evolutionary psychology. In: *Handbook of evolutionary psychology*, ed. D. M. Buss, pp. 68–95. Wiley. [LB, aMDG]

Kappeler, P. M. & Pereira, M. E., eds. (2003) *Primate life histories and socioecology*. The University of Chicago Press. [DM]

Karavasilis, L., Doyle, A. B. & Markiewicz, D. (2003) Associations between parenting style and attachment to mother in middle childhood and adolescence. *International Journal of Behavioral Development* 27:153–64. [aMDG]

Kardia, S. R., Chu, J. & Sowers, M. R. (2006) Characterizing variation in sex steroid hormone pathway genes in women of 4 races/ethnicities: The study of women's health across the nation (SWAN). *American Journal of Medicine* 119:s3–s15. [rMDG]

Karishma, K. K. & Herbert, J. (2002) Dehydroepiandrosterone (DHEA) stimulates neurogenesis in the hippocampus of the rat, promotes survival of newly formed neurons and prevents corticosterone-induced suppression. *European Journal of Neuroscience* 16:445–53. [MVF]

Kenrick, D. T., Ackerman, J. M. & Ledlow, S. (2003) Evolutionary social psychology: Adaptive predispositions and human culture. In: *Handbook of social psychology*, ed. J. DeLamater, pp. 103–22. Kluwer Academic/Plenum Press. [JMA]

Kenrick, D. T., Sundie, J. M. & Kurzban, R. (2008) Cooperation and conflict between kith, kin, and strangers: Game theory by domains. In: *Foundations of evolutionary psychology*, ed. C. Crawford & D. Krebs, pp. 353–70. Erlbaum. [JMA]

Kerns, K. A. (2008) Attachment in middle childhood. In: *Handbook of attachment: Theory, research, and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [LB, KAK]

Kerns, K. A., Abraham, M. M., Schlegelmilch, A. & Morgan, T. A. (2007) Mother-child attachment in later middle childhood: Assessment approaches and associations with mood and emotion regulation. *Attachment and Human Development* 9:33–53. [aMDG, MJB-K]

Kerns, K. A. & Richardson, R. A., eds. (2005) *Attachment in middle childhood.* Guilford Press. [rMDG]

Kerns, K. A., Schlegelmilch, A., Morgan, T. A. & Abraham, M. M. (2005) Assessing attachment in middle childhood. In: *Attachment in middle childhood*, ed. L. A. Kerns & R. A. Richardson, pp. 46–70. Guilford Press. [aMDG, KAK]

Kerns, K. A., Tomich, P. L., Aspelmeier, J. E. & Contreras, J. M. (2000) Attachment-based assessments of parent-child relationships in middle childhood. *Developmental Psychology* 36:614–26. [B-BC, aMDG]

Kerns, K. A., Tomich, P. L. & Kim, P. (2006) Normative trends in perceptions of availability and utilization of attachment figures in middle childhood. *Social Development* 15:1–22. [KAK]

Keverne, E. B., Nevison, C. M. & Martel, F. L. (1999) Early learning and the social bond. In: *The integrative neurobiology of affiliation*, ed. C. S. Carter & I. I. Lederhendler, pp. 263–74. MIT Press. [aMDG]

Kimonides, V. G., Spillantini, M. G., Sofroniew, M. V., Fawcett, J. W. & Herbert, J. (1999) Dehydroepiandrosterone antagonizes the neurotoxic effects of corticosterone and translocation of stress-activated protein kinase 3 in hippocampal primary cultures. *Neuroscience* 89:429–36. [MVF]

Kirk, K. M., Blomberg, S. P., Duffy, D. L., Heath, A. C., Owens, I. P. F. & Martin, N. G. (2001) Natural selection and quantitative genetics of life-history traits in western women: A twin study. *Evolution* 55:423–35. [aMDG]

Kirkpatrick, L. A. (1998) Evolution, pair bonding, and reproductive strategies: A reconceptualization of adult attachment. In: *Attachment theory and close relationships*, ed. J. A. Simpson & W. S. Rholes, pp. 353–93. Guilford Press. [aMDG]

Kirkpatrick, L. A. & Davis, K. E. (1994) Attachment style, gender and relationship stability: A longitudinal analysis. *Journal of Personality and Social Psychology* 66:502–12. [aMDG, LP, VZ]

Kobak, R., Rosenthal, N., Zajac, K. & Madsen, S. D. (2007) Adolescent attachment hierarchies and the search for an adult pair bond. *New Directions for Child and Adolescent Development* 117:57–72. [DKS]

Kokko, H. (1997) Evolutionary stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology* 41:99–107. [aMDG]

Kokko, H. & Jennions, M. (2003) It takes two to tango. *Trends in Ecology and Evolution* 18:103–104. [rMDG]

(2008) Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* 21:919–48. [rMDG]

Korte, S. M., Koolhaas, J. M., Wingfield, J. C. & McEwen, B. S. (2005) The Darwinian concept of stress: Benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neuroscience and Biobehavioral Reviews* 29:3–38. [aMDG]

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. & Fehr, E. (2005) Oxytocin increases trust in humans. *Nature* 435:673–76. [rMDG]

Kramer, K. L. (2005) Children's help and the pace of reproduction: Cooperative breeding in humans. *Evolutionary Anthropology* 14:224–37. [aMDG]

Kruger, D. J. (2008) Women's life history attributes are associated with preferences in mating relationships. *Evolutionary Psychology* 6:245–58. [rMDG]

Labrie, F., Belanger, A., Luu-The, V., Labrie, C., Simard, J., Cusan, L., Gomez, J. L. & Candas, B. (1998) DHEA and the intracrine formation of androgens and estrogens in peripheral target tissues: Its role during aging. *Steroids* 63: 322–28. [MVF]

Labrie, F., Luu-The, V., Belanger, A., Lin, S. G., Simard, J., Pelletier, G. & Labrie, C. (2005) Is dehydroepiandrosterone a hormone? *Journal of Endocrinology* 187:169–96. [aMDG]

Lamb, M. E., Frodi, A. M., Hwang, C. P. & Frodi, M. (1982) Varying degrees of paternal involvement in infant care: Attitudinal and behavioral correlates. In: *Nontraditional families: Parenting and child development*, ed. M. E. Lamb, pp. 117–37. Erlbaum. [aMDG]

Lampert, A. & Friedman, A. (1992) Sex differences in vulnerability and maladjustment as a function of parental investment: An evolutionary approach. *Social Biology* 39:65–81. [aMDG]

Lancaster, J. B. (1989) Evolutionary and cross-cultural perspectives on single-parenthood. In: *Sociobiology and the social sciences*, ed. R. Bell & N. Bell. Texas Tech University Press. [aMDG]

Landolt, M. A., Lalumiere, M. L. & Quinsey, V. L. (1995) Sex differences in intra-sex variation in human mating tactics: An evolutionary approach. *Ethology and Sociobiology* 16:3–23. [aMDG]

LeBlanc, A. N. (2004) *Random family: Love, drugs, trouble and coming of age in the Bronx.* HarperPerennial. [AC]

Leckman, J. F., Carter, C. S., Hennessy, M. B., Hrdy, S. B., Keverne, E. B., Klann-Delius, G., Schradin, C., Todt, D. & von Holst, D. (2005) Biobehavioral processes in attachment and bonding. In: *Attachment and bonding: A new synthesis*, ed. C.S. Carter, L. Ahnert, K. E. Grossmann, S. B. Hrdy, M. E. Lamb, S. W. Porges & N. Sachser, pp. 301–48. MIT Press. [aMDG]

Lehnart, J. & Neyer, F. J. (2006) Should I stay or should I go? Attachment and personality in romantic relationships across young adulthood. *European Journal of Personality* 20:475–95. [LP]

Lenton, A., Penke, L., Todd, P. M. & Fasolo, B. (in press) The heart does have its reasons: Social rationality in mate choice. In: *Social rationality*, ed. R. Hertwig, U. Hoffrage & the ABC Research Group. Oxford University Press. [LP]

Lewis, M., Feiring, C. & Rosenthal, S. (2000) Attachment over time. *Child Development* 71:707–20. [aMDG]

Levine, R. & Norman, K. (2001) The infant's acquisition of culture: Early attachment reexamined in anthropological perspective. In: *The psychology of cultural experience*, ed. C. Moore & H. Mathews, pp. 83–104. Cambridge University Press. [RJQ]

Li, N. P. & Kenrick, D. T. (2006) Sex similarities and differences in preferences for short-term mates: What, whether, and why. *Journal of Personality and Social Psychology* 90:468–89. [JMA]

Li, T. (2005) Patterns of attachment in adulthood and rearing style. *Chinese Journal of Behavioral Medical Science* 15:149–50. [NL]

(2006) Some hot topics in attachment theory: Comment on Hu & Meng. *Acta Scientiarum Naturalium Universitatis Pekinensis* 42:18–25. [NL]

Li, T. & Du, S. (2005) Analysis of adult attachment style of 50 surgery patients. *Chinese Journal of Clinical Psychology* 13:417–19. [NL]

Li, T., He, J., Guo, X. & Lu, X. (2006a) Adult attachment and social support of self-learning students. *Chinese Journal of Behavioral Medical Science* 15:1019–20. [NL]

Li, T. & Kato, K. (2006) Measuring adult attachment: validation of ECR in Chinese sample. *Acta Psychologica Sinica* 38:399–406. [NL]

Li, T., Li, J., Qin, H., Guo, X., Wang, X. & Liu, Z. (2008) Adult attachment and mental health in Chinese college students. *Chinese Mental Health Journal* 22:631–35. [NL]

Li, T., Li, N. & Li, M. (2006b) Correlation of adult attachment with social support and subjective well-being. *Chinese Journal of Clinical Rehabilitation* 10:47–49. [NL]

Li, T., Li, N. & Zhu, Y. (2007) Adult attachment and subjective well-being of Chinese college students. *Chinese Journal of Behavioral Medical Science* 16:54–56. [NL]

Li, T., Wang, X. & Guo, X. (2006c) Attachment style and dyadic heterosexual interaction behavior among junior high school students. *Chinese Journal of Behavioral Medical Science* 15:644–46. [NL]

Lieberman, M., Doyle, A. & Markiewicz, D. (1999) Developmental patterns in security of attachment to mother and father in late childhood and early adolescence: Associations with peer relations. *Child Development* 70:202–13. [aMDG]

Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M. & Perrett, D. I. (2002) Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society B (Biological Sciences)* 269:1095–1100. [LEV]

Little, A. C. & Mannion, H. (2006) Viewing attractive or unattractive same-sex individuals changes self-rated attractiveness and face preferences in women. *Animal Behaviour* 72:981–87. [LEV]

Liu, Y. (2007) An examination of three models of the relationships between parental attachment and adolescents' social functioning and depressive symptoms. *Journal of Youth and Adolescence*. 37:941–52. [aMDG]

Locke, J. L., & Bogin, B. (2006) Language and life history: A new perspective on the development and evolution of human language. *Behavioral and Brain Sciences* 29:259–80. [rMDG]

Low, B. (2000) Sex, wealth, and fertility: Old rules, new environments. In: *Adaptation and human behavior: An anthropological perspective*, ed. L. Cronk, N. Chagnon & W. Irons, pp. 323–44. Aldine De Gruyter. [aMDG]

Lynch, M. (1987) Evolution of intrafamilial interactions. *Proceedings of the National Academy of Sciences USA* 84:8507–11. [aMDG]

Lyons-Ruth, K., Bronfman, E. & Parsons, E. (1999) Frightened, frightening, and atypical maternal behavior and disorganized infant attachment strategies. In: *Atypical patterns of infant attachment*, ed. J. Vondra & D. Barnett. *Monographs of the Society for Research in Child Development, No. 64*, pp. 67–96. [aMDG]

Lyons-Ruth, K. & Jacobvitz, D. (1999) Attachment disorganization: Unresolved loss, relational violence, and lapses in behavioral and attentional strategies. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver, pp. 520–54. Guilford. [aMDG, AJL]

Maccoby, E. E. (1991) Different reproductive strategies in males and females. *Child Development* 62:676–81. [aMDG]

Mace, R. (2000a) An adaptive model of human reproductive rate where wealth is inherited: Why people have small families. In: *Adaptation and human behavior: An anthropological perspective*, ed. L. Cronk, N. Chagnon & W. Irons, pp. 283–322. Aldine De Gruyter. [aMDG]

(2000b) Evolutionary ecology of human life history. *Animal Behaviour* 59:1–10. [aMDG]

Mace, R. & Sear, R. (2005) Are humans cooperative breeders? In: *Grandmotherhood. The evolutionary significance of the second half of female life*, ed. E. Voland, A. Chasiotis & W. Schiefenhoevel, pp. 143–59. Rutgers University Press. [aMDG]

Maestripieri, D. (2003) Attachment. In: *Primate psychology*, ed. D. Maestripieri, pp. 108–43. Harvard University Press. [DM]

(2005a) Effects of early experience on female behavioural and reproductive development in rhesus macaques. *Proceedings of the Royal Society of London B* 272:1243–48. [DM]

(2005b) On the importance of comparative research for the understanding of human behavior and development: A reply to Gottlieb & Lickliter (2004). *Social Development* 14:181–86. [DM]

Maestripieri, D. & Roney, J. R. (2006) Evolutionary developmental psychology: Contributions from comparative research with nonhuman primates. *Developmental Review* 26:120–37. [DM]

Maestripieri, D., Roney, J. R., DeBias, N., Durante, K. M. & Spaepen, G. M. (2004) Father absence, menarche, and interest in infants among adolescent girls. *Developmental Science* 7:560–66. [DM]

Main, M. (1981) Avoidance in the service of attachment: a working paper. In: *Behavioral development: The Bielefeld Interdisciplinary Project*, ed. K. Immelmann, G. Barlow, M. Main & L. Petrinovich, pp. 651–93. Cambridge University Press. [aMDG]

(1990) Cross-cultural strategies of attachment and attachment organization: Recent studies, changing methodologies, and the concept of conditional strategies. *Human Development* 33:48–61. [aMDG]

Main, M. & Cassidy, J. (1988) Categories of response to reunion with the parent at age six: Predictable from infant attachment classification and stable over a 1-month period. *Developmental Psychology* 24:415–526. [MJB-K]

Main, M. & Goldwyn, R. (1998) Adult attachment scoring and classification system. Unpublished manuscript, University of California at Berkeley. [aMDG]

Main, M. & Hesse, E. (1990) Parent's unresolved traumatic experiences are related to infant disorganized attachment status: Is frightened and/or frightening parental behavior the linking mechanism? In: *Attachment in the preschool years: Theory, research, and intervention*, ed. M. Greenberg, D. Cicchetti & E. M. Cummings. The University of Chicago Press. [aMDG]

Main, M., Hesse, E. & Kaplan, N. (2005) Predictability of attachment behavior and representational processes at 1, 6, and 19 years of age. In: *Attachment from infancy to adulthood. The major longitudinal studies*, ed. K. E. Grossmann, K. Grossmann & E. Waters, pp. 245–304. Guilford Press. [rMDG]

Main, M., Kaplan, N. & Cassidy, J. (1985) Security in infancy, childhood and adulthood: A move to the level of representation. In: *Growing points in attachment theory and research*, ed. I. Bretherton & E. Waters. *Monographs of the Society for Research in Child Development* 50(1–2, Serial No. 209), pp. 66–106. [MJB-K]

Main, M. & Solomon, J. (1990) Procedures for identifying infants as disorganized/disoriented during Ainsworth Strange Situations. In: *Attachment in the pre-school years: Theory, research and intervention*, ed. M. T. Greenberg, D. Cicchietti, & E. M. Cummings, pp. 121–60. Chicago University Press. [AJL]

Majewska, M., Demigoren, S., Spivak, C. E. & London, E. D. (1990) The neurosteroid dehydroepiandrosterone sulfate is an allosteric antagonist of the GABAa receptor. *Brain Research* 526:143–46. [MVF]

Marazziti, D., Dell'Osso, B., Baroni, S., Mungai, F., Catena, M. & Rucci, P. (2006) A relationship between oxytocin and anxiety of romantic attachment. *Clinical Practice and Epidemiology in Mental Health* 2:28. [rMDG]

Marlowe, F. (2000) Paternal investment and the human mating system. *Behavioural Processes* 51:45–61. [arMDG]

(2003) The mating system of foragers in the Standard Cross-Cultural Sample. *Cross-Cultural Research* 37:282–306. [arMDG]

Mazur, A. & Booth, A. (1998) Testosterone and dominance in men. *Behavioral and Brain Sciences* 21:353–97. [rMDG]

McCarthy, M. M. (1995) Estrogen modulation of oxytocin and its relation to behavior. In: *Oxytocin: Cellular and molecular approaches in medicine and research*, ed. R. Ivell & J. Russell, pp. 235–42. Plenum Press. [aMDG]

McCarthy, M. M., McDonald, C. H., Brooks, P. J. & Goldman, D. (1996) An anxiolytic action of oxytocin is enhanced by estrogen in the mouse. *Physiology and Behavior* 60:1209–15. [aMDG]

McClintock, M. & Herdt, G. (1996) Rethinking puberty: The development of sexual attraction. *Current Directions in Psychological Science* 5:178–83. [aMDG]

McNamara, J. M. & Houston, A. I. (1996) State-dependent life histories. *Nature* 380:215–21. [aMDG]

Meadows-Oliver, M., Lois, S. S., Swartz, M. K. & Ryan-Krause, P. (2007) Sources of stress and support and maternal resources of homeless teenage mothers. *Journal of Child and Adolescent Psychiatric Nursing* 20(2):116–25. [MJK]

Meaney, M. J. & Szyf, M. (2005) Environmental programming of stress responses through DNA methylation: Life at the interface between a dynamic environment and a fixed genome. *Dialogues in Clinical NeuroSciences* 7(2):103–23. [SGF]

Mellen, S. L. W. (1981) *The evolution of love.* Freeman. [rMDG]

Mendle, J., Turkheimer, E., D'Onofrio, B. M., Lynch, S. K., Emery, R. E., Slutske, W. S. & Martin, N. G. (2006) Family structure and age at menarche: a children-of-twins approach. *Developmental Psychology* 42:533–42. [JRH]

Micheal, A., Jenaway, A., Paykel, E. S. & Herbert, J. (2000) Altered salivary dehydroepiandrosterone levels in major depression in adults. *Biological Psychiatry* 48:989–95. [MVF]

Mikulincer, M. (2006) Attachment, caregiving, and sex within romantic relationships: A behavioral systems perspective. In: *Dynamics of romantic love: Attachment, caregiving, and sex*, ed. M. Mikulincer & G. S. Goodman, pp. 23–46. Guilford Press. [DKS]

Mikulincer, M. & Goodman, G. S., eds. (2006) *Dynamics of romantic love: Attachment, caregiving, and sex.* Guilford Press. [DKS]

Miller, E. M. (1994) Paternal provisioning versus mate seeking in human populations. *Personality and Individual Differences* 17: 227–55. [aMDG]

Miller, G. (2000) *The mating mind. How sexual choice shaped the evolution of human nature*. Heinemann. [rMDG]

Miller, L. C., Bard, K. A., Juno, C. J. & Nadler, R. D. (1986) Behavioral responsiveness of young chimpanzees (*Pan troglodytes*) to a novel environment. *Folia Primatologica (Basel)* 47(2–3):128–42. [LJS]

Mock, D. & Parker, G. (1997) *The evolution of sibling rivalry.* Oxford University Press. [aMDG]

Moffitt, T. E., Caspi, A. & Belsky, J. (1992) Childhood experience and the onset of menarche: A test of a sociobiological model. *Child Development* 63:47–58. [aMDG]

Morison, P. & Masten, A. S. (1991) Peer reputation in middle childhood as a predictor of adaptation in adolescence: A seven-year follow-up. *Child Development* 62:991–1007. [aMDG]

Moss, E., Cyr, C. & Dubois-Comtois, K. (2004) Attachment at early school age and developmental risk: Examining family contexts and behavior problems of controlling-caregiving, controlling-punitive, and behaviorally disorganized children. *Developmental Psychology* 40:519–32. [KAK]

Moss, E., Rousseau, D., Parent, S., St-Laurent, D. & Saintonge, J. (1998) Correlates of attachment at school age: Maternal reported stress, mother-child interaction, and behavior problems. *Child Development* 69:1390–1405. [aMDG]

Moss, E., St-Laurent, D., Dubois-Comtois, K. & Cyr, C. (2005) Quality of attachment at school age. In: *Attachment in middle childhood*, ed. K. A. Kerns & R. A. Richardson, pp. 189–211. Guilford. [rMDG]

Muehlenbein, M. P. & Bribiescas, R. G. (2005) Testosterone-mediated immune functions and male life histories. *American Journal of Human Biology* 17:527–58. [MVF]

Muehlenbein, M. P., Richards, R. J., Campbell, B. C., Phillippi, K. M., Murchison, M. A., Myers, L. & Svec, F. (2003) Dehydroepiandrosterone-sulfate as a biomarker of senescence in male non-human primates. *Experimental Gerontology* 38:1077–85. [MVF]

Nakao, T. & Kato, K. (2003) How do adult attachment scales relate to one another?: The correspondence between four category and three category scales. *Kyushu University Psychological Research* 4:57–66. [NL]

Neberich, W., Lehnart, J., Penke, L. & Asendorpf, J. B. (in press) Family of origin, age at menarche, and reproductive strategies: A test of four evolutionary-developmental models. *European Journal of Developmental Psychology*. [LP]

Nettle, D. (2006) The evolution of personality variation in humans and other animals. *American Psychologist* 61:622–31. [aMDG, JRH]

(2007) Individual differences. In: *Oxford handbook of evolutionary psychology*, ed. R. Dunbar & L. Barrett, pp. 479–90. Oxford University Press. [aMDG]

Nguyen, A. D. & Conley, A. J. (2008) Adrenal androgens in humans and non-human primates: Production, zonation, and regulation. In: *Disorders of the human adrenal cortex*, ed. C.E. Flück & W. L. Miller. Special issue of *Endocrine Development* 13:33–54. [MVF]

Noftle, E. E. & Shaver, P. R. (2006) Attachment dimensions and the big five personality traits: Associations and comparative ability to predict relationship quality. *Journal of Research in Personality* 40:179–208. [rMDG]

O'Connor, T. G. & Byrne, J. G. (2007) Attachment measures for research and practice. *Child and Adolescent Mental Health* 12:187–92. [DKS]

O'Connor, T. G. & Croft, C. M. (2001) A twin study of attachment in preschool children. *Child Development* 72:1501–11. [aMDG]

O'Connor, T. G., Croft, C. M. & Steele, H. (2000) The contributions of behavioural genetic studies to attachment theory. *Attachment and Human Development* 2:107–22. [aMDG]

Ong, K. K., Potau, N., Petry, C. J., Jones, R., Ness, A. R., ALSPAC Study Team, Honour, J. W., de Zegher, F., Ibanez, L. & Dunger, D. B. (2004) Opposing influences of prenatal and postnatal weight gain on adrenarche in normal boys and girls. *Journal of Clinical Endocrinology and Metabolism* 89:2647–51. [MVF]

Orcutt, H., Garcia, M. & Pickett, S. (2005) Female-perpetrated intimate partner violence and romantic attachment style in a college student sample. *Violence and Victims* 20:287–302. [AC, rMDG]

Orentreich, N., Brind, J. L., Rizer, R. L. & Vogelman, J. H. (1984) Age changes and sex differences in serum dehydroepiandrosterone sulfate concentrations throughout adulthood. *Journal of Clinical Endocrinology and Metabolism* 59:551–55. [MVF]

Overall, N. C. & Sibley, C. G. (2008) Attachment and attraction toward romantic partners versus relevant alternatives in daily interactions. *Personality and Individual Differences* 44:1126–37. [rMDG]

Palmert, M. R., Hayden, D. L., Mansfield, J., Crigler, J. F., Crowley, W. F., Chandler, D. W. & Boepple, P. A. (2001) The longitudinal study of adrenal maturation during gonadal suppression: Evidence that adrenarche is a gradual process. *Journal of Clinical Endocrinology and Metabolism* 86:4536–42. [MVF, aMDG]

Panksepp, J. (1998) *Affective neuroscience: The foundations of human and animal emotions*. Oxford University Press. [aMDG]

Pannebakker, F. (2007) Morality from infancy to middle childhood. Unpublished doctoral dissertation, Faculty of Social and Behavioral Sciences, Leiden University, The Netherlands. [rMDG, MJB-K]

Parent, A. S., Teilmann, G., Juul, A., Skakkebaek, N. E., Toppari, J. & Bourgignon, J. P. (2003) The timing of normal puberty and the age limits of sexual precocity: Variations around the world, secular trends, and changes after migration. *Endocrine Reviews* 24:668–93. [rMDG]

Parker, G. A., Royle, N. J. & Hartley, I. R. (2002) Intrafamilial conflict and parental investment: A synthesis. *Philosophical Transactions of the Royal Society of London B* 357:295–307. [aMDG]

Parker, J. G., Low, C. M., Walker, A. R. & Gamm, B. K. (2005) Friendship jealousy in young adolescents: Individual differences and links to sex, self-esteem, aggression, and social adjustment. *Developmental Psychology* 41:235–50. [AC]

Pedersen, C. A., Ahnert, L., Anzenberger, G., Belsky, J., Draper, P., Fleming, A. S., Grossmann, K., Sachser, N., Sommer, S., Tietze, D. P. & Young, L. J. (2005) Beyond infant attachment: The origins of bonding in later life. In: *Attachment and bonding: A new synthesis*, ed. C.S. Carter, L. Ahnert, K. E. Grossmann, S. B. Hrdy, M. E. Lamb, S.W. Porges & N. Sachser, pp. 385–428. MIT Press. [aMDG]

Pellegrini, A. D. (1995) A longitudinal study of boys' rough-and-tumble play and dominance during early adolescence. *Journal of Applied Developmental Psychology* 16:77–93. [aMDG]

Pellegrini, A. D. & Bartini, M. (2001) Dominance in early adolescent boys: Affiliative and aggressive dimensions and possible functions. *Merrill-Palmer Quarterly* 47:142–63. [aMDG]

Penke, L. & Asendorpf, J. B. (in press) Beyond global sociosexual orientations: A more differentiated look at sociosexuality and its effects on courtship and romantic relationships. *Journal of Personality and Social Psychology*. [rMDG, LP]

Penke, L., Denissen, J. J. A. & Miller, G. F. (2007a) Evolution, genes, and inter-disciplinary personality research. *European Journal of Personality* 21:639–65. [LP]

(2007b) The evolutionary genetics of personality. *European Journal of Personality* 21:549–87. [LP]

Penke, L., Todd, P. M., Lenton, A. & Fasolo, B. (2007c) How self-assessments can guide human mating decisions. In: *Mating intelligence: Sex, relationships, and the mind's reproductive system*, ed. G. Geher & G. F. Miller, pp. 37–75. Erlbaum. [LP]

Pennington, R. & Harpending, H. (1988) Fitness and fertility among Kalahari !Kung. *American Journal of Physical Anthropology* 77:303–19. [aMDG]

Penton-Voak, I. S., Jacobson, A. & Trivers, R. (2004) Populational differences in attractiveness judgements of male and female faces: Comparing British and Jamaican samples. *Evolution and Human Behavior* 25:355–70. [LEV]

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. (1999) Menstrual cycle alters face preference. *Nature* 399:741–42. [LEV]

Petters, D. (2006a) Designing agents to understand infants. Unpublished PhD thesis in Cognitive Science, Department of Computer Science, University of Birmingham. Available at: http://www.cs.bham.ac.uk/~ddp/petters-phd-2006.pdf. [DP]

(2006b) Implementing a theory of attachment: A simulation of the strange situation with autonomous agents. In: *Proceedings of the Seventh International Conference on Cognitive Modelling*, ed. D. Fum, F. D. Missier & A. Stocco, pp. 226–31. Edizioni Golardiche. Available at: http://www.cs.bham.ac.uk/~ddp/pettersiccm.pdf. [DP]

Phillips, D. I. W. (2007) Programming of the stress response: A fundamental mechanism underlying the long-term effects of fetal environment? *Journal of Internal Medicine* 261:453–60. [SGF]

Pianka, E. R. (1970) On r- and K-selection. *American Naturalist* 104:592–96. [DJK]

Picardi, A., Caroppo, E., Toni, A., Binetti, D. & Di Maria, G. (2005) Stability of attachment-related anxiety and avoidance and their relationships with the five-factor model and the psychobiological model of personality. *Psychology and Psychotherapy: Theory, Research and Practice* 78:327–45. [rMDG]

Picardi, A., Vermigli, P., Toni, A., D'Amico, R., Bitetti, D. & Pasquini, P. (2002) Further evidence of the validity of the Italian version of the questionnaire "Experiences in Close Relationships" (ECR), a self-report instrument to assess adult attachment. *Italian Journal of Psychopathology* 8. (Online publication). [aMDG]

Pigliucci, M. (2005) Evolution of phenotypic plasticity: Where are we going now? *Trends in Ecology and Evolution* 20:481–86. [LP]

Pinker, S. (1997) *How the mind works*. Norton. [aMDG]

Pressler, J. L. & Hepworth, J. T. (2002) A quantitative use of the NIDCAP tool: The effect of gender and race on very preterm neonate's behavior. *Clinical Nursing Research* 11(1):89–102. [SGF]

Promislow, D. & Harvey, P. (1990) Living fast and dying young: A comparative analysis of life-history variation among mammals. *Journal of the Zoological Society of London* 220:417–37. [aMDG]

(1991) Mortality rates and the evolution of mammal life histories. *Acta Oecologica* 12:119–37. [aMDG]

Provost, M. P., Troje, N. F. & Quinsey, V. L. (2008) Short-term mating strategies and attraction to masculinity in point-light walkers. *Evolution and Human Behavior* 29:65–69. [LEV]

Quinlan, R. J. (2003) Father absence, parental care, and female reproductive development. *Evolution and Human Behavior* 24:376–90. [CDG]

(2006) Gender and risk in a matrifocal Caribbean community. *American Anthropologist* 108(3):464–79. [RJQ]

(2007) Human parental effort and environmental risk. *Proceedings of the Royal Society of London B* 274:121–25. [arMDG]

Quinlan, R. J. & Flinn, M. V. (2003) Intergenerational transmission of conjugal stability. *Journal of Comparative Family Studies* 34:569–84. [MVF]

Quinlan, R. J. & Quinlan, M. B. (2007a) Evolutionary ecology of human pair-bonds. Cross-cultural tests of alternative hypotheses. *Cross-Cultural Research* 41:149–69. [aMDG]

(2007b) Parenting and cultures of risk: A comparative analysis of infidelity, aggression, and witchcraft. *American Anthropologist* 109:164–79. [aMDG]

Quinlan, R. J., Quinlan, M. B. & Flinn, M. V. (2003) Parental investment and age at weaning in a Caribbean village. *Evolution and Human Behavior* 24:1–16. [MVF]

(2005) Local resource enhancement and sex-biased breastfeeding in a Caribbean community. *Current Anthropology* 46(3):411–31. [RJQ]

Quirin, M., Pruessner, J. C. & Kuhl, J. (2008) HPA system regulation and adult attachment anxiety: individual differences in reactive and awakening cortisol. *Psychoneuroendocrinology*. 33:581–90. [rMDG]

Rainey, W. E., Carr, B. R., Sasano, H., Suzuki, T. & Mason, J. I. (2002) Dissecting human adrenal androgen production. *Trends in Endocrinology and Metabolism* 13:234–39. [MVF]

Remer, T., Boye, K. R., Hartmann, M. F. & Wudy, S. A. (2005) Urinary markers of adrenarche: Reference values in healthy subjects, aged 3–18 years. *Journal of Clinical Endocrinology and Metabolism* 90(4):2015–21. [MVF]

Renken, B., Egeland, B., Marvinney, D., Manglesdorf, S. & Sroufe, L. A. (1989) Early childhood antecedents of aggression and passive-withdrawal in early elementary school. *Journal of Personality* 57:257–81. [aMDG]

Rodkin, P. C., Farmer, T. W., Ruth, P. & Acker, R. V. (2006) They're cool: Social status and peer group support for aggressive boys and girls. *Social Development* 15:175–204. [aMDG]

Roff, D. A. (2002) *Life history evolution*. Sinauer. [aMDG]

Roisman, G. I., Holland, A., Fortuna, K., Fraley, C., Clausell, E. & Clarke, A. (2007) The Adult Attachment Interview and self-reports of attachment style: An empirical reapprochement. *Journal of Personality and Social Psychology* 92:678–97. [arMDG]

Roney, J. R. & Maestripieri, D. (2002) The importance of comparative and phylogenetic analyses in the study of adaptation. *Behavioral and Brain Sciences* 25:525. [DM]

Rose, A. J. & Rudolph, K. D. (2006) A review of sex differences in peer relationship processes: Potential trade-offs for the emotional and behavioral development of girls and boys. *Psychological Bulletin* 132:98–131. [AC]

Roth, G. & Dicke, U. (2005) Evolution of the brain and intelligence. *Trends in Cognitive Sciences* 9(5):250–57. [MVF]

Rowe, D. C. (2000a) Environmental and genetic influences on pubertal development: evolutionary life history traits? In: *Genetic influences on human fertility and sexuality: recent empirical and theoretical findings*, ed. J. L. Rodgers, D. C Rowe & W. B. Miller, pp. 147–68. Kluwer. [aMDG]

(2000b) Evolutionary ecology embraces early experience. *Evolution and Human Behavior* 21:352–64. [JRH]

Rowe, D. C., Vazsonyi, A. T. & Figueredo, A. J. (1997) Mating-effort in adolescence: A conditional or alternative strategy. *Personality and Individual Differences* 23:105–15. [aMDG]

Rutter, M., Moffitt, T. E. & Caspi, A. (2006) Gene-environment interplay and psychopathology: Multiple varieties but real effects. *Journal of Child Psychology and Psychiatry* 47:226–61. [rMDG]

Rutter, M., Pickles, A., Murray, R. & Eaves, L. (2001) Testing hypotheses on specific environmental causal effects on behavior. *Psychological Bulletin* 127:291–324. [rMDG]

Sadalla, E. I., Kenrick, D. T. & Vershure, B. (1987) Dominance and heterosexual attraction. *Journal of Personality and Social Psychology* 52:730–38. [aMDG]

Sagi, A., Lamb, M. E., Lewkowicz, K. S., Shoham, R., Dvir, R. & Estes, D. (1985) Security of infant-mother, -father, and -*metapelet* attachment among kibbutz-reared Israeli children. *Monographs of the Society for Research in Child Development* 50:257–75. [aMDG]

Sagi, A., van IJzendoorn, M. H., Aviezer, O., Donnell, F. & Mayseless, O. (1994) Sleeping out of home in a kibbutz communal arrangement: It makes a difference for infant-mother attachment. *Child Development* 65:992–1004. [aMDG]

Sanders, K. A. & Bruce, N. W. (1997) A prospective study of psychosocial stress and fertility in women. *Human Reproduction* 12:2324–29. [rMDG]

Santner, S. J., Albertson, B., Zhang, G., Zhang, G., Santulli, M., Wang, C., Demers, L. M., Shackleton, C. & Santen, R. J. (1998) Comparative rates of androgen production and metabolism in Caucasian and Chinese subjects. *Journal of Clinical Endocrinology and Metabolism* 83:2104–109. [rMDG]

Saudino, K. J. (1997) Moving beyond the heritability question: New directions in behavioral genetic studies of personality. *Current Directions in Psychological Science* 6:86–90. [JRH]

Scarr, S. (1992) Developmental theories for the 1990s: Development and individual differences. *Child Development* 63:1–19. [rMDG]

Schachner, D. A. & Shaver, P. R. (2002) Attachment style and human mate poaching. *New Review of Social Psychology* 1:122–29. [aMDG, VZ]

(2004) Attachment dimensions and motives for sex. *Personal Relationships* 11:179–95. [VZ]

Schaller, M. & Murray, D. R. (2008) Pathogens, personality and culture: Disease prevalence predicts worldwide variability in sociosexuality, extraversion, and openness to experience. *Journal of Personality and Social Psychology* 95:212–21. [LP]

Scharfe, E. & Bartholomew, K. (1994) Reliability and stability of adult attachment patterns. *Personal Relationships* 1:23–43. [aMDG]

Schmitt, D. P. (2005a) Is short-term mating the maladaptive result of insecure attachment? A test of competing evolutionary perspectives. *Personality and Social Psychology Bulletin* 31:747–68. [aMDG, LP]

(2005b) Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences* 28:247–75; discussion 275–311. [LB, rMDG, LP]

(2008) Evolutionary perspectives on romantic attachment and culture: How ecological stressors influence dismissing orientations across genders and geographies. *Cross-Cultural Research* 42:220–47. [rMDG]

Schmitt, D. P., Alcalay, L., Allensworth, M., Allik, J., Ault, L., Austers, I., Bennett, K. L., Bianchi, G., Boholst, F., Borg Cunen, M. A., Braeckman, J., Brainerd Jr., E. G., Caral, L. G. A., Caron, G., Casullo, M. M., Cunningham, M., Daibo, I., De Backer, C., De Souza, E., Diaz-Loving, R., Diniz, G., Durkin, K., Echegaray, M., Eremsoy, E., Euler, H. A., Falzon, R., Fisher, M. L., Fowler, R., Fry, D. P., Fry, S., Ghayur, M. A., Giri, V. N., Golden, D. L., Grammer, K., Grimaldi, L., Halberstadt, J., Haque, S., Hefer, E., Herrera, D., Hertel, J., Hitchell, A., Hoffman, H., Hradilekova, Z., Hudek-Kene-evi, J., Huffcutt, A., Jaafar, J., Jankauskaite, M., Kabangu-Stahel, H., Kardum, I., Khoury, B., Kwon, H., Laidra, K., Laireiter, A., Lakerveld, D., Lampart, A., Lauri, M., Lavallée, M., Lee, S., Leung, L.C., Locke, K. D., Locke, V., Luksik, I., Magaisa, I., Marcinkeviciene, J., Mata, A., Mata, R., McCarthy, B., Mills, M. E., Mkhize, N. J., Moreira, J., Moreira, S., Moya, M., Munyea, M., Noller, P., Olimat, H., Opre, A., Panayiotou, A., Petrovic, N., Poels, K., Popper, M., Poulimenou, M., P'yatokha, V., Raymond, M., Reips, U., Reneau, S. E., Rivera-Aragon, S., Rowatt, W. C., Ruch, W., Rus, V. S., Safir, M. P., Salas, S., Sambataro, F., Sandnabba, K. N., Schleeter, R., Schulmeyer, M. K., Schütz, A., Scrimali, T., Shackelford, T. K., Sharan, M. B., Shaver, P. R., Sichona, F., Simonetti, F., Sineshaw, T., Sookdew, R., Speelman, T., Sümer, H. C., Sümer, N., Supekova, M., Szlendak, T., Taylor, R., Timmermans, B., Tooke, W., Tsaousis, I., Tungaraza, F. S. K., Turner, A., Vandermassen, G., Vanhoomissen, T., Van Overwalle, F., Van Wesenbeek, I., Vasey, P. L., Verissimo, J., Voracek, M., Wan, W. W. N., Wang, T., Weiss, P., Wijaya, A., Woertment, L., Youn, G. & Zupanèiè, A. (2003a) Are men universally more dismissing than women? Gender differences in romantic attachment across 62 cultural regions. *Personal Relationships* 10:307–31. [arMDG, LP]

Schmitt, D. P., Alcalay, L., Allik, J., Ault, L., Austers, I., Bennett, K. L., Bianchi, G., Boholst, F., Borg Cunen, M. A., Braeckman, J., Brainerd Jr., E. G., Caral, L. G. A., Caron, G., Casullo, M. M., Cunningham, M., Daibo, I., De Backer, C., De Souza, E., Diaz-Loving, R., Diniz, G., Durkin, K., Echegaray, M., Eremsoy, E., Euler, H. A., Falzon, R., Fisher, M. L., Foley, D., Fry, D. P., Fry, S., Ghayur, M. A., Golden, D. L., Grammer, K., Grimaldi, L., Halberstadt, J., Herrera, D., Hertel, J., Hoffman, H., Hradilekova, Z., Hudek-Kene-evi, J., Jaafar, J., Jankauskaite, M., Kabangu-Stahel, H., Kardum, I., Khoury, B., Kwon, H., Laidra, K., Laireiter, A., Lakerveld, D., Lampart, A., Lauri, M., Lavallée, M., Lee, S., Leung, L.C., Locke, K. D., Locke, V., Luksik, I., Magaisa, I., Marcinkeviciene, J., Mata, A., Mata, R., McCarthy, B., Mills, M. E., Moreira, J., Moreira, S., Moya, M., Munyea, M., Noller, P., Opre, A., Panayiotou, A., Petrovic, N., Poels, K., Popper, M., Poulimenou, M., P'yatokha, V., Raymond, M., Reips, U., Reneau, S. E., Rivera-Aragon, S., Rowatt, W. C., Ruch, W., Rus, V. S., Safir, M. P., Salas, S., Sambataro, F., Sandnabba, K. N., Schulmeyer, M. K., Schütz, A., Scrimali, T., Shackelford, T. K., Shaver, P. R., Sichona, F., Simonetti, F., Sineshaw, T., Sookdew, R., Speelman, T., Spyrou, S., Sümer, H.C., Sümer, N., Supekova, M., Szlendak, T., Taylor, R., Timmermans, B., Tooke, W., Tsaousis, I., Tungaraza, F. S. K., Vandermassen, G., Vanhoomissen, T., Van Overwalle, F., Vanwesenbeek, I., Vasey, P. L., Verissimo, J., Voracek, M., Wan, W. W. N., Wang, T., Weiss, P., Wijaya, A., Woertment, L., Youn, G., & Zupanèiè, A. (2003b) Universal sex differences in the desire for sexual variety: Tests from 52 nations, 6 continents, and 13 islands. *Journal of Personality and Social Psychology* 85:85–104. [aMDG, LP]

Schmitt, D. P., Alcalay, L., Allensworth, M., Allik, J., Ault, L., Austers, I., et al. Bennett, K. L., Bianchi, G., Boholst, F., Borg Cunen, M. A., Braeckman, J., Brainerd E. G. Jr., Caral, L. Caron, G., G. A., Casullo, M. M., Cunningham, M., Daibo, I., De Backer, C., De Souza, E., Diaz-Loving, R., Diniz, G., Durkin, K., Echegaray, M., Eremsoy, E., Euler, H. A., Falzon, R., Fisher, M. L., Foley, D., Fowler, R., Fry, D. P., Fry, S., Ghayur, M. A., Giri, V. N., Golden, D. L., Grammer, K., Grimaldi, L. Halbertandt, J., Haque, S., Herrera, D., Hertel, J., Hitchell, A., Hoffmann, H., Hooper, D., Hradilekova, Z., Hudek-Kene-Evi, J., Huffcutt, A., Jaafar, J., Jankauskaite, M., Kabangu-Stahel, H., Kardum, I., Khoury, B., Kwon, H., Laidra, K., Laireiter, A., Lakerveld, D., Lampert, A., Lauri, M., Lavallée, M., Lee, S., Leung, L. C., Locke, K. D., Locke, V., Luksik, I., Magaisa, I., Marcinkeviciene, D., Mata, A., Mata, R., McCarthy, B., Mills, M. E., Mkhize, N. J:, Moreira, J., Moreira, S., Moya, M., Munyae, M., Noller, P., Olimat, H., Opre, A., Panayiotou, A., Petrovic, N., Poels, K., Popper, M., Poulimenou, ., P'Yatokha, V., Raymond, M., Reips, U., Reneau, S., Rivera-Aragon, S., Rowatt, W. C., Ruch, W., Rus, V. S., Safir, M. P., Salas, S., Sambataro, F., Sandnabba, K. N., Schleeter, R., Schulmeyer, M. K., Schütz, A., Scrimali, T., Shackelford, T. K., Sharan, M. B., Shaver, P. R., Sichona, F., Simonetti, F., Sineshaw, T., Sookdew, R., Speelman, T., Spyrou, S., Sümer, H. C., Sümer, N., Supekova, M., Szlendak, T., Taylor, R., Timmermans, B., Tooke, W., Tsaousis, I., Tungaraza, F. S. K., Turner, A., Vandermassen, G., Vanhoomissen, T., van Overwalle, F., Vanwesenbeeck, I., vasey, P. L., Verissimo, J., Voracek., M., Wan, W. W. N., Wang, T., Weiss, P., Wijaya, A., Woertman, L., Youn, G., Zupanèiè, A. (2004) Patterns and universals of adult romantic attachment across 62 cultural regions. Are models of self and others pancultural constructs? *Journal of Cross-Cultural Psychology* 35:367–402. [arMDG]

Schwartz, J. P., Lindley, L.D. & Buboltz Jr., W. C. (2007) Adult attachment orientations: Relation to affiliation motivation. *Counselling Psychology Quarterly* 20:253–65. [rMDG]

Serbin, L. A., Powlishta, K. K. & Gulko, J. (1993) The development of sex typing in middle childhood. *Monographs of the Society for Research in Child Development* 64: 1–74. [aMDG]

Shaver, P. R., Belsky, J. & Brennan, K. A. (2000) Comparing measures of adult attachment: An examination of interview and self-report methods. *Personal Relationships* 7:25–43. [aMDG]

Shaver, P. R. & Mikulincer, M. (2002) Attachment-related psychodynamics. *Attachment and Human Development* 4:133–61. [aMDG]

Shemmings, D. (2006) Using adult attachment theory to differentiate adult children's internal working models of later life filial relationships. *Journal of Aging Studies* 20:177–91. [NL]

Shrewsbury, V. & Wardle, J. (2008) Socioeconomic status and adiposity in childhood: A systematic review of cross-sectional studies 1990–2005. *Obesity* 16:275–84. [JRH]

Sibley, C. G. & Overall, N. C. (2008) Modeling the hierarchical structure of attachment representations: A test of domain differentiation. *Personality and Individual Differences* 44:238–49. [aMDG]

Siever, L. J. (2008) Neurobiology of aggression and violence. *American Journal of Psychiatry* 165:429–42. [AC]

Simon, N. G. & Lu, S. (2006) Androgens and aggression. In: *Biology of aggression*, ed. R. J. Nelson, pp. 211–30. Oxford University Press. [aMDG]

Simpson, J. A. (1994) Pair bonding as an organizational model for integrating research on close relationships. *Psychological Inquiry* 5:58–61. [aMDG]

(1999) Attachment theory in modern evolutionary perspective. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

Simpson, J. A. & Belsky, J. (2008) Attachment theory within a modern evolutionary framework. In *Handbook of attachment: Theory, research, and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [LB]

Simpson, J. A. & Gangestad, S. W. (1991) Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology* 60:870–83. [rMDG]

Simpson, J. A. & Rholes, W. S. (2002) Fearful-avoidance, disorganization, and multiple working models: Some directions for future theory and research. *Attachment and Human Development* 4:223–29. [arMDG]

Simpson, J. A., Wilson, C. L. & Winterheld, H. A. (2004) Sociosexuality and romantic relationships. In: *The handbook of sexuality in close relationships*, ed. J. H. Harvey, A. Wenzel & S. Sprecher. Erlbaum. [rMDG]

Solomon, J. & George, C. (1999) The measurement of attachment security in infancy and childhood. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

Spear, L. P. (2000) The adolescent brain and age-related behavioral manifestations. *Neuroscience and Biobehavioral Review* 24:417–63. [aMDG]

Sroufe, L. A. (2003) Attachment categories as reflections of multiple dimensions. Comment on Fraley and Spieker (2003). *Developmental Psychology* 39:413–16. [aMDG]

Sroufe, L. A., Bennett, C., Englund, M., Urban, J. & Shulman, S. (1993) The significance of gender boundaries in preadolescence: Contemporary correlates and antecedents of boundary violation and maintenance. *Child Development* 64:455–66. [aMDG, MJK]

Staller, K. M. (2004) Runaway youth system dynamics: A theoretical framework for analyzing runaway and homeless youth policy. *Families in Society* 85(3):379–90. [MJK]

Strous, R. D., Spivak, B., Yoran-Hegesh, R., Maayan, R., Averbuch, E., Kotler, M., Mester, R. & Weizman, A. (2001) Analysis of neurosteroid levels in attention deficit hyperactivity disorder. *The International Journal of Psychopharmacology* 4:259–64. [aMDG]

Suess, G. J., Grossmann, K. E. & Sroufe, L. A. (1992) Effects of infant attachment to mother and father on quality of adaptation in preschool: From dyadic to individual organisation of self. *International Journal of Behavioral Development* 15:43–65. [aMDG]

Sulcova, J., Hill, M., Hampl, R. & Starka, L. (1997) Age and sex related differences in serum levels of unconjugated dehydroepiandrosterone and its sulfate in normal subjects. *Journal of Endocrinology* 154:57–62. [MVF]

Suomi, S. J. (1999) Attachment in rhesus monkeys. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

Svensson, E. & Sheldon, B. C. (1998) The social context of life history evolution. *Oikos* 83:466–77. [aMDG]

Szielasko, A. L., Symons, D. K. & Price, L. (2007) The role of attachment in adolescent sexual risk-taking. Paper presented at the Annual Convention of the Canadian Psychological Association, Ottawa, Ontario, 2007. [DKS]

Szielasko, A. L., Symons, D. K. & Price, E. L. (under review) Attachment styles in sexual and romantic relationships predict invasive sexual behaviors and approaches. [DKS]

Tanner, J. M. (1978) *Fetus into man: Physical growth from conception to maturity.* Harvard University Press. [MVF]

Target, M., Fonagy, P. & Shmueli-Goetz, Y. (2003) Attachment representations in school-age children: The development of the Child Attachment Interview (CAI). *Journal of Child Psychotherapy* 29:171–86. [KAK]

Taylor, S. E. (2006) Tend and befriend: Biobehavioral bases of affiliation under stress. *Current Directions in Psychological Science* 15:273–77. [aMDG]

Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenenwald, T. L., Gurung, R. A. & Updegraff, J. A. (2000) Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review* 107:411–29. [aMDG]

Thiessen, D. (1994) Environmental tracking by females: Sexual lability. *Human Nature* 5:167–202. [JJJ]

Thompson, R. A. (1999) Early attachment and later development. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

Tinbergen, N. (1963) On aims and methods in ethology. *Zeitschrift für Tierpsychologie* 20:410–33. [DJK]

Tither, J. M. & Ellis, B. J. (2008) Impact of fathers on daughters' age at menarche: A genetically- and environmentally-controlled sibling study. *Developmental Psychology* 44:1409–20. [rMDG]

Todd, P. M., Penke, L., Fasolo, B. & Lenton, A. P. (2007) Different cognitive processes underlie human mate choices and mate preferences. *Proceedings of the National Academy of Sciences USA* 104:15011–16. [LP]

Tomaszycki, M. L., Davis, J. E., Gouzoules, H. & Wallen, K. (2001) Sex differences in infant rhesus macaque separation–rejection vocalizations and effects of prenatal androgens. *Hormones and Behavior* 39:267–76. [aMDG]

Tooby, J. & Cosmides, L. (2005) Conceptual foundations of evolutionary psychology. In: *The handbook of evolutionary psychology*, ed. D. M. Buss, pp. 5–67. Wiley. [LP]

Torgersen, A. M., Grova, B. K. & Sommersted, R. (2007) A pilot study of attachment patterns in adult twins. *Attachment and Human Development* 9:127–38. [aMDG]

Toth, I., Szollosi, A., Danis, I., Green, J. & Gervai, J. (2006) Changes of attachment to the mother from infancy to childhood: Girls are less at risk? *Infant Mental Health Journal* 27:343. [arMDG]

Townsend, J. M. (1995) Sex without emotional involvement: An evolutionary interpretation of sex differences. *Archives of Sexual Behavior* 24:173–76. [rMDG]

(2005) Sex, sex differences, and the new polygyny. *Behavioral and Brain Sciences* 28:295–96. [rMDG]

Tracy, J. L., Shaver, P. R., Albino, A. W. & Cooper, M. L. (2003) Attachment styles and adolescent sexuality. In: *Adolescent romance and sexual behavior: Theory, research, and practical implications*, ed. P. Florsheim. Erlbaum. [rMDG, VZ]

Treboux, D., Crowell, J. A. & Waters, E. (2004) When "new" meets "old": Configurations of adult attachment representations and their implications for marital functioning. *Developmental Psychology* 40:295–314. [aMDG]

Treloar, S. A. & Martin, N. G. (1990) Age at menarche as a fitness trait: Nonadditive genetic variance detected in a large twin sample. *American Journal of Human Genetics* 47:137–48. [aMDG]

Trivers, R. L. (1971) The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57. [CDG]

(1972) Parental investment and sexual selection. In: *Sexual selection and the descent of man 1871–1971*, ed. B. Campbell, pp. 136–79. Aldine. [arMDG]

(1974) Parent-offspring conflict. *American Zoologist* 14:249–64. [aMDG]

(1985) *Social evolution*. Benjamin/Cummings. [aMDG]

Trivers, R. L. & Willard, D. E. (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92. [AJL, RJQ]

Troy, M. & Sroufe, L. A. (1987) Victimization among preschoolers: Role of attachment relationship history. *Journal of the American Academy of Child and Adolescent Psychiatry* 26:166–72. [aMDG]

True, M. M. (1994) Mother-infant attachment and communication among the Dogon of Mali. Unpublished doctoral thesis. University of California at Berkeley. [rMDG]

Turkheimer, E. (2004) Spinach and ice cream: Why social science is so difficult. In: *Behavior genetics principles: Perspectives in development, personality, and psychopathology*, ed. L. F. DiLalla. American Psychological Association. [rMDG]

Turner, P. J. (1991) Relations between attachment, gender, and behavior with peers in preschool. *Child Development* 62:1475–88. [aMDG]

Uchino, B. N., Cacioppo, J. T. & Kiecolt-Glaser, J. K. (1996) The relationship between social support and physiological processes: A review with emphasis on underlying mechanisms and implications for health. *Psychological Bulletin* 119:488–531. [VZ]

van Goozen, S. H. M., Matthys, W., Cohen-Kettenis, P. T., Thijssen, J. H. H. & van Engeland, H. (1998) Adrenal androgens and aggression in conduct disorder prepubertal boys and normal controls. *Biological Psychiatry* 43:156–58. [aMDG]

van Goozen, S. H. M., van den Ban, E., Matthys, W., Cohen-Kettenis, P. T., Thijssen, J. H.H. & van Engeland, H. (2000) Increased adrenal androgen functioning in children with oppositional defiant disorder: A comparison with psychiatric and normal controls. *Journal of the American Academy of Children and Adolescent Psychiatry* 39:1446–51. [aMDG]

Van IJzendoorn, M. H. (2000) The similarity of siblings' attachments to their mother. *Child Development* 71:1086–98. [aMDG]

Van IJzendoorn, M. H. & Bakermans-Kranenburg, M. J. (1996) Attachment representations in mothers, fathers, adolescents, and clinical groups: A meta-analytic search for normative data. *Journal of Consulting and Clinical Psychology* 64:8–21. [aMDG, MJB-K]

(2006) DRD4 7-repeat polymorphism moderates the association between maternal unresolved loss or trauma and infant disorganization. *Attachment and Human Development* 8:291–307. [rMDG]

(2008) The distribution of adult attachment representations in clinical groups: Meta-analytic search for patterns of attachment. In: *The Adult Attachment Interview in clinical context*, ed. H. Steele & M. Steele, pp. 69–98. Guilford. [MJB-K]

(in preparation) Distributions of adult attachment representations in clinical and non-clinical groups: A meta-analysis. [MJB-K]

Van IJzendoorn, M. H. & Sagi, A. (1999) Cross-cultural patterns of attachment: Universal and contextual dimensions. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver, pp. 713–34. Guilford Press. [aMDG, JH]

Van IJzendoorn, M. H., Schuengel, C. & Bakermans-Kranenburg, M. J. (1999) Disorganized attachment in early childhood: Meta-analysis of precursors, concomitants, and sequelae. *Development and Psychopathology* 11:225–49. [AJL]

Van IJzendoorn, M. H., Vereijken, C. M. J. L., Bakermans-Kranenburg, M. J. & Riksen-Walraven, J. M. A. (2004) Is the Attachment Q-Sort a valid measure of attachment security in young children? *Child Development* 75:1188–1213. [MJB-K]

Veith, J. L., Buck, M., Getzlaf, S., Van Dalfsen, P. & Slade, S. (1983) Exposure to men influences the occurrence of ovulation in women. *Physiology and Behavior* 31:313–15. [VZ]

Verschueren, K. & Marcoen, A. (1999) Representation of self and socioemotional competence in kindergartners: Differential and combined effects of attachment to mother and to father. *Child Development* 70:183–201. [aMDG, MJB-K]

(2002) Perceptions of self and relationship with parents in aggressive and nonaggressive rejected children. *Journal of School Psychology* 40:501–22. [aMDG]

Viau, V. (2002) Functional cross-talk between the hypothalamic-pituitary-gonadal and -adrenal axes. *Journal of Neuroendocrinology* 14:506–13. [aMDG]

Vitzthum, V. J. (2008) Evolutionary models of women's reproductive functioning. *Annual Review of Anthropology*. 37:53–73. [rMDG]

Voland, E. (1998) Evolutionary ecology of human reproduction. *Annual Review of Anthropology* 27:347–74. [aMDG]

Vondra, J. I., Hommerding, K. D. & Shaw, D. S. (1999) Stability and change in infant attachment in a low-income sample. *Monographs of the Society for Research in Child Development* 64:119–44. [aMDG]

Wakefield, J. C. (2005) Biological function and dysfunction. In: *The handbook of evolutionary psychology*, ed. D. M. Buss. Wiley. [AJL]

Wallen, K. (2005) Hormonal influences on sexually differentiated behavior in nonhuman primates. *Frontiers of Neuroendocrinology* 26:7–26. [aMDG]

Wan, L. & Li, T. (in press) Adult attachment and handling interpersonal conflict of employees. *Chinese Journal of Clinical Rehabilitation.* [NL]

Wang, C., Christenson, P. & Swerdloff, R. (2007) Clinical relevance of racial and ethnic differences in sex steroids. *Journal of Clinical Endocrinology and Metabolism* 92:2433–35. [rMDG]

Wang, E., Ding, Y. C., Flodman, P., Kidd, J. R., Kidd, K. K., Grady, D. L., Ryder, O. A., Spence, M. A., Swanson, J. M. & Moyzis, R. K. (2004) The genetic architecture of selection at the human dopamine receptor D4 (*DRD4*) gene locus. *American Journal of Human Genetics* 74:931–44. [rMDG]

Wang, Y. & Ollendick, T. H. (2001) A cross-cultural and developmental analysis of self-esteem in Chinese and Western children. *Clinical Child and Family Psychology Review* 4:253–71. [NL]

Wasser, S. K. & Barash, D. P. (1983) Reproductive suppression among female mammals: Implications for biomedicine and sexual selection theory. *The Quarterly Review of Biology* 58:513–38. [arMDG]

Wasser, S. K. & Place, N. J. (2001) Reproductive filtering and the social environment. In: *Reproductive ecology and human evolution*, ed. P. Ellison, pp. 137–57. Aldine De Gruyter. [rMDG]

Waters, E. (2002) *Live long and prosper*. Available at: http://www.psychology.sunysb.edu/attachment/gallery/live_long/live_long.html. [DP]

Waters, E., Crowell, J., Elliot, M., Corcoran, D. & Treboux, D. (2002) Bowlby's secure base theory and the social/personality psychology of attachment styles: Work(s) in progress. *Attachment and Human Development* 4:230–42. Available at: www.psychology.sunysb.edu/attachment/online/waters_ahd_comment.pdf. [DP]

Waters, E. & Beauchaine, T. P. (2003) Are there really patterns of attachment? Comment on Fraley and Spieker (2003). *Developmental Psychology* 39:417–22. [aMDG]

Waters, E., Merrick, S., Treboux, D., Crowell, J. & Albersheim, L. (2000) Attachment security in infancy and early adulthood: a twenty-year longitudinal study. *Child Development* 71:684–89. [aMDG]

Waters, E., Weinfield, N. S. & Hamilton, C. E. (2000) The stability of attachment security from infancy to adolescence to early adulthood: General discussion. *Child Development* 71:703–06. [aMDG]

Watson, D., Klohnen, E. C., Casillas, A., Simms, E. N., Haig, J. & Berry, D. S. (2004) Match makers and deal breakers: Analyses of assortative mating in newlywed couples. *Journal of Personality* 72:1029–68. [rMDG]

Weeden, J., Cohen, A. B. & Kenrick, D. T. (2008) Religious attendance as reproductive support. *Evolution and Human Behavior* 29:327–34. [JMA]

Weinfield, N. S., Sroufe, L. A., Egeland, B. & Carlson, E. A. (1999) The nature of individual differences in infant-caregiver attachment. In: *Handbook of attachment: Theory, research and clinical applications*, ed. J. Cassidy & P. R. Shaver. Guilford. [aMDG]

(2000) Attachment from infancy and adulthood in a high-risk sample: Continuity, discontinuity, and their correlates. *Child Development* 71:695–702. [aMDG]

Weinstock, M. (2005) The potential influence of maternal stress hormones on development and mental health of the offspring. *Brain, Behavior and Immunity* 19:296–308. [MVF]

Weisfeld, G. E. (1999) *Evolutionary principles of human adolescence*. Basic Books. [aMDG]

Weisfeld, G. E., Bloch, S. A. & Ivers, J. W. (1983) A factor analytic study of peer-perceived dominance in adolescent boys. *Adolescence* 18:229–43. [aMDG]

Weisfeld, G. E., Muczenski, Weisfeld & Omark (1987) Stability of boys' social success among peers over an eleven-year period. In: *Interpersonal relations: Family, peers, friends*, ed. J. A. Meacham. Karger. [aMDG]

West-Eberhard, M. J. (2003) *Developmental plasticity and evolution*. Oxford University Press. [MVF, arMDG, LP]

Wilkins, A. S. (2002) *The evolution of developmental pathways*. Sinauer. [aMDG]

Williams, G. C. (1966) *Adaptation and natural selection*. Princeton University Press. [JMA]

Wilson, E. O. (1975) *Sociobiology: The new synthesis*. Harvard University Press. [DJK]

(1998) *Consilience: The unity of knowledge*. Knopf. [rMDG]

Wilson, M. & Daly, M. (1985) Competitiveness, risk-taking, and violence: The young male syndrome. *Ethology and Sociobiology* 6:59–73. [aMDG]

Winking, J., Kaplan, H., Gurven, M. & Rucas, S. (2007) Why do men marry and why do they stray? *Proceedings of the Royal Society of London. B*. 274:1643–49. [aMDG]

Wright, J. D. (1990) Poor people, poor health: The health status of the homeless. *Journal of Social Issues* 46:49–64. [MJK]

Xu, A., Xie, X., Liu, W., Xia, Y. & Liu, D. (2007) Chinese family strengths and resiliency. *Marriage and Family Review* 41:143–64. [NL]

Zak, P. J., Kurzban, R. & Matzner, W. T. (2005) Oxytocin is associated with human trustworthiness. *Hormones and Behavior* 48:522–27. [rMDG]

Zemel, B. S. & Katz, S. H. (1986) The contribution of adrenal and gonadal androgens to the growth in height of adolescent males. *American Journal of Physical Anthropology* 71:459–66. [MVF]

Ziegler, T. E., Savage A., Scheffler G. & Snowdon, C. T. (1987) The endocrinology of puberty and reproductive functioning in female cotton-top tamarins *(Saguinus oedipus)* under varying social conditions. *Biology of Reproduction* 37(3):618–27. [LJS]

Ziv, Y., Aviezer, O., Gini, M., Sagi, A., Karie, N. K. & Korean-Karie, N. (2000) Emotional availability in the mother-infant dyad as related to the quality of infant-mother attachment relationship. *Attachment and Human Development* 2(2):149–69. [MJK]