

Chapter 5

Attachment Theory within a Modern Evolutionary Framework

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It has often been assumed that animals were in the first place rendered social, and that they feel as a consequence uncomfortable when separated from each other, and comfortable whilst together, but it is a more probable view that these sensations were first developed in order that those animals which would profit by living in society, should be induced to live together, . . . for with those animals which were benefited by living in close association, the individuals which took the greatest pleasure in society would best escape various dangers; whilst those that cared least for their comrades and lived solitary would perish in greater numbers.

—CHARLES DARWIN (1871, Vol. 1, p. 80)

As this quotation indicates, Charles Darwin was an attachment theorist. Although he focused on “society” (instead of significant others) and “comrades” (instead of attachment figures), Darwin was the first scientist to appreciate the full extent to which human social nature is a product of selection pressures. John Bowlby, who not only admired Darwin’s theoretical vision but was one of his biographers (see Bowlby, 1991), spent most of his brilliant career treading the intellectual path that Darwin started paving. Integrating ideas from Darwin’s theory of evolution by natural selection, object relations theory, control systems theory, evolutionary biology, and the fields of ethology and cognitive psychology, Bowlby (1969/1982, 1973, 1980) developed a grand synthesis of social and personality development across the lifespan, which is now known as attachment theory. One

reason why attachment theory is so generative and prominent today is its deep intellectual ties to fundamental principles of evolution.

In many respects, however, attachment theory and its adherents have not kept up with developments in evolutionary biology. In fact, beyond acknowledging that attachment behavior evolved via natural selection to facilitate the survival of infants in the environment of evolutionary adaptedness (EEA), surprisingly little attachment-related research and writing addresses the importance of either reproduction and reproductive fitness as the target of natural selection or the role of environmental conditions, including parenting, in regulating the development of reproductive strategies. These are critical issues that we address in this chapter.

As we shall see, attachment theory is one of a handful of major middle-level evolutionary theo-

ries. Bowlby's interest in the cognitive, emotional, and behavioral ties that bind humans to one another began with an astute observation. Across all human cultures and most primate species, young and vulnerable infants display a specific sequence of reactions following separation from their stronger, older, and wiser caregivers. Immediately following separation, most infants *protest*, typically crying, screaming, and throwing temper tantrums as they search for their caregivers. Bowlby surmised that vigorous protest during the early phases of caregiver absence is a good initial strategy to promote survival. Intense protests usually draw the attention of caregivers to their infants, who, during evolutionary history, would have been susceptible to injury or predation if left unattended.

If loud and persistent protests fail to retrieve the caregiver, infants enter a second stage, *despair*, during which their movement declines and they fall silent. From an evolutionary standpoint, Bowlby realized that despondency is a good "second" strategy to promote survival. Excessive movement could result in accident or injury, and loud protests combined with movement may draw predators. Thus, if protests fail to retrieve the caregiver, the next best survival strategy would be to avoid actions that might increase the risks of self-inflicted harm or predation.

Bowlby also observed that, after a period of despair, infants who are not reunited with their caregivers enter a third stage: *detachment*. During this phase, the infant begins to resume normal activity without the caregiver, learning to behave in an independent and self-reliant manner. Bowlby (1969/1982) conjectured that the function of detachment is to permit the formation of emotional bonds with new caregivers. He reasoned that emotional ties with previous caregivers must be relinquished before new bonds can be formed. From the standpoint of evolution, detachment allows infants to cast off old emotional ties and begin the process of forming new ones with caregivers who may be willing to provide the attention and resources necessary for survival.

Bowlby believed that the cognitive, emotional, and behavioral reactions that characterize each stage reveal the operation of an innate attachment system. The main reason why the attachment system evolved and remains so deeply ingrained in human nature is that it provided a good solution to one of the most difficult adaptive problems our ancestors faced—how to increase the probability of survival through the most perilous years of social and physical development. Inspired

by Darwin, Bowlby believed that the attachment system was genetically "wired" into many species through directional selection during evolutionary history.

There were, of course, limitations to Bowlby's and other early attachment theorists' understanding and application of evolutionary thinking, many of which Bowlby sought to correct as he developed attachment theory (see Belsky, 1999; Simpson, 1999). One shortcoming was his initial focus on the differential survival of species rather than individuals. Another shortcoming was his focus on the survival function of attachment rather than the implications it has for differential reproduction. To enhance reproductive fitness, individuals must not only survive to reproductive age, but they also must successfully mate and raise children, who then must mate and raise their own children, and so on. Fortunately, as we shall see, some contemporary attachment theorists have shifted attention to how attachment phenomena and processes in childhood are systematically linked to the enactment of different reproductive strategies in adulthood (Belsky, in press; Belsky, Steinberg, & Draper, 1991; Chisholm, 1996, 1999). However, because individuals cannot reproduce without first surviving to reproductive age, Bowlby wisely built the foundation of attachment theory on this vital precursor to ultimate reproductive fitness.

Early attachment theorists also held the erroneous view that most rearing environments in the EEA were benign, resulting in the secure attachment pattern being "species-typical" (e.g., Ainsworth, 1979; Main, 1981). The EEA, however, was not nearly as uniform, resource-rich, or benign as many early attachment theorists envisioned (e.g., Edgerton, 1992), which means that no single attachment pattern should have been primary or species-typical. In fact, as we shall see, the adoption of different attachment patterns (in children) or orientations (in adults) most likely reflect evolved, often unconsciously enacted tactics that probably improved *reproductive fitness* in response to the specific environments in which individuals grew and developed in ancestral times and perhaps still today. Reproductive fitness reflects the extent to which an individual's genes are present in his or her descendants. The concept of inclusive fitness (described below) highlights the important distinction between genes present in direct descendants (i.e., children) and those present in indirect descendants (e.g., grandchildren, nieces, nephews). From an evolutionary standpoint, the

maximization of reproductive or inclusive fitness is the goal of all living organisms, including humans, and thus is the target of natural selection.

Perhaps the biggest impediment to Bowlby's understanding of evolution, however, was the undeveloped state of evolutionary thinking when he began formulating attachment theory in the 1950s and 1960s. The foundation of attachment theory was well established long before several significant "middle-level" theories of evolution—theories that address the major adaptive problems with which humans were confronted during our evolutionary history—were introduced in the 1970s. As a consequence, Bowlby was not privy to much of what is now known as the "modern" evolutionary perspective when he started erecting the tenets of attachment theory. Until recently, few of the modern middle-level evolutionary theories were systematically linked with mainstream attachment theory and research. We hope to facilitate this process.

The overarching goal of this chapter is to place attachment theory in a modern (neo-Darwinian) evolutionary perspective. The chapter had seven sections. The first briefly reviews theoretical developments that have transformed Darwin's (1859, 1871) original theory of natural selection into the modern evolutionary perspective. We also discuss where attachment theory fits within the hierarchy of evolutionary principles and middle-level theories. The second section describes the major adaptive problems that our ancestors had to overcome given the probable nature of the environments they inhabited in the course of the past 100,000 years, focusing on the most stable features of the social EEAs that humans probably inhabited.

The third section addresses how the two major components of attachment theory—the normative component and the individual-difference component—fit within a modern evolutionary view of human behavior. In discussing normative attachment, we briefly review the species-typical course through which attachment bonds develop across the lifespan. Different patterns or styles of attachment are construed as adaptive, ecologically contingent behavioral strategies that should have facilitated reproduction in adulthood given the probable environments that individuals would inhabit as adults.

Section four reveals how another major middle-level theory of evolution—Trivers's (1974) theory of parent-offspring conflict—sheds new light on several attachment-related phenomena,

including how and why parents and children negotiate issues of weaning, parental investment, and the child's eventual independence. In the fifth section, we review and evaluate several attachment/life history models, most of which articulate how and why different attachment patterns in childhood might affect the trajectory of social and personality development, culminating in divergent reproductive strategies in adulthood. In the final two sections, we discuss some unresolved issues and promising new directions for research, and offer concluding comments.

The Place of Attachment Theory in Modern Evolutionary Thinking

Though it remains one of the greatest intellectual accomplishments in the history of science, Darwin's (1859) original theory of evolution was incomplete and imprecise. Darwin's thinking was constrained by several factors. First, his theory predated our understanding of genes and patterns of inheritance. Second, because Darwin did not focus on genes as the principal units on which natural selection operates, he could not explain why some organisms engage in self-sacrificial or nonreproductive behavior. This enigma was not solved until Hamilton (1964) introduced the concept of *inclusive fitness* (i.e., the notion that differential gene replication is what truly drives evolution). Third, Darwin had only a faint understanding of how sexual recombination and genetic mutations provide the variation from which better adaptations and new species are selected. Fourth, he did not fully appreciate the degree to which specific adaptations have both benefits and costs. Similar to many theorists of his time, Darwin focused more on the benefits bestowed by certain adaptations, without fully factoring in their associated costs (Cronin, 1991). Darwin's brilliance, however, allowed him to envision how natural selection might operate *without* the benefits of all this later knowledge.

The Rise of Modern Evolutionary Theories

Few theoretical advances occurred in the evolutionary sciences for more than a century after Darwin published his second landmark book, *The Descent of Man, and Selection in Relation to Sex*, in 1871. This state of affairs changed in the mid-

1960s. With the development of inclusive fitness theory, Hamilton (1964) introduced kin selection. By focusing on the gene rather than the individual organism as the primary unit on which selection operates, Hamilton solved the biggest paradox that Darwin never unraveled, namely, that during the evolutionary struggle for reproductive fitness, some organisms forgo reproduction to assist the reproductive efforts of their biological relatives.

Hamilton solved this riddle by realizing that an individual's total (inclusive) fitness depends on his or her own reproductive output plus the total reproductive output of all kin who share some portion of the individual's genes. If genes are the units on which selection operates, and if individuals can facilitate the reproductive output of their biological relatives, there would be situations in which it would pay to sacrifice one's own reproductive output, including one's life, to facilitate the reproduction of close relatives. Unlike Darwin, Hamilton could calculate the degree to which pairs of individuals are likely to share novel genes. On average, parents share half of their genes with their children, full siblings share half of their genes with each other, grandparents share one-fourth of their genes with their grandchildren, aunts and uncles share one-fourth of their genes with their nieces and nephews, and first cousins share one-eighth of their genes.

Armed with this knowledge, Hamilton confirmed that self-sacrificial behavior could have been selected in situations where the costs of engaging in an act were less than the benefits to be gained times the degree to which individuals were biologically related (i.e., altruistic behavior should occur when $C < Br$, where C = costs, B = benefits, and r = the degree of relatedness; see Simpson, 1999). For example, while it would make sense to sacrifice one's own life to save at least two biological children (each of whom shares 50% of the parent's genes), one would have to save many more nieces or nephews (who carry fewer genes) to achieve the same fitness benefits. Hamilton's intellectual breakthrough marked the dawn of the modern evolutionary perspective. Indeed, inclusive fitness theory is the overarching theory of natural selection from which virtually all middle-level evolutionary theories are derived. Although Hamilton's research was not cited by Bowlby (1969/1982), Bowlby's first major statement on attachment proved to be one of the first middle-level evolutionary theories. In developing attachment theory, Bowlby sought to understand and explain how our ancestors successfully solved

the first major barrier to inclusive fitness—how to survive the perils and dangers of infancy.

Several important theoretical advances followed in the 1970s, many of which were spearheaded by Robert Trivers. In 1971, he introduced the theory of reciprocal altruism, which explains why organisms with inherently "selfish" genes should, at times, behave cooperatively with non-kin. The development of this theory was important for attachment theory given the presumed links between early attachment security–insecurity and the development of empathy and prosocial behavior. Trivers identified some of the specific conditions under which selective reciprocal altruism ought to enhance an individual's inclusive fitness. Axelrod (1984) then demonstrated mathematically how a quid pro quo strategy of helping others (i.e., a tit-for-tat strategy) can evolve and become stable amid other competing strategies.

In 1972, Trivers unveiled the theory of parental investment and sexual selection. According to this theory, different amounts of parental investment in children govern sexual selection, which explains why females and males in many species differ on certain physical attributes (e.g., relative body size) and behavioral characteristics (e.g., aggressiveness). Trivers argued that, in species in which one sex *initially* invests more time, effort, resources, and energy in producing and raising offspring (usually women, in the case of humans), the other sex (usually men) should compete to mate with the higher-investing sex. The intense *intrasexual* competition that results should have produced some of the modal physical, behavioral, and emotional differences witnessed between the sexes. This leads one to wonder whether we should expect similarities or differences in attachments to mothers versus fathers.

In 1974, Trivers introduced the theory of parent–offspring conflict, which explains why parents and their children—individuals who share half their genes and, thus, should be jointly invested in passing them on to future generations—experience conflict: Their individual self-interests are not identical. Because this theory has several fascinating implications for how attachment patterns between children and their caregivers can be understood, it is discussed in greater detail below. For now, though, it is important to recognize that this theoretical precept challenges the common assumption that parents are motivated to be unconditionally devoted to their offspring rather than "strategic allocators" of time, attention, and other resources.

In recent years, life history theory (Charnov, 1993; Kaplan & Gangestad, 2005) has become a unifying perspective within the evolutionary sciences. To leave descendants, individuals must solve multiple problems associated with survival, growth, development, and reproduction across the lifespan. Depending on life circumstances, an individual's time, effort, and energy can be allotted to *somatic effort* (i.e., investing in growth and development of one's own body to facilitate survival enroute to later reproduction) or *reproductive effort* (i.e., funneling effort toward progeny). Reproductive effort has two components: *mating effort* (i.e., locating, courting, and retaining suitable mates) and *parenting effort* (i.e., gestating, giving birth, postnatal child care, and teaching/socialization). Life history theory explains how individuals should best allocate somatic versus reproductive effort given their past, current, and anticipated (future) life circumstances, as well as their health and well-being.

Attachment Theory in the Hierarchy of Evolutionary Theories

Inclusive fitness theory, which encompasses both Darwin's concept of fitness due to one's own reproduction (i.e., direct descendants: children) and Hamilton's notion of fitness due to the reproduction of one's biological relatives (i.e., indirect descendants: grandchildren, nieces, etc.), is the superordinate theory of evolution from which all middle-level evolutionary theories flow. The middle-level theories, which include reciprocal altruism (Trivers, 1971), sexual selection and parental investment (Trivers, 1972), parent-offspring conflict (Trivers, 1974), and attachment (Bowlby 1969/1982), address the specific adaptive problems that humans faced and had to resolve during evolutionary history. Thus, they reside one level below inclusive fitness theory. Because life history theory addresses how individuals should allocate their finite resources across the entire lifespan, it interconnects and integrates the middle-level theories. Each middle-level theory in turn has a small set of basic principles that reside at the next level down (see Simpson, 1999). Most evolutionary hypotheses and predictions are derived from these basic principles.

Sexual selection and parental investment theory, for instance, contains two major principles relevant to mate selection. The theory suggests that the search for mates is governed by the degree to which prospective mates (1) are likely

to be good investors in and providers for future offspring, and (2) have desirable attributes (e.g., physical attractiveness or other mate-attracting features) that could be passed on genetically to offspring (Gangestad & Simpson, 2000). Specific predictions and hypotheses are then derived from each of these principles.

Attachment theory also has two primary theoretical components. The *normative component* of attachment theory makes predictions about relatively universal, stable patterns of behavior, particularly in response to situations in which individuals feel ill, fatigued, afraid, or upset (Bowlby, 1969/1982). The *individual-difference component* offers predictions about the ontogenic origins and developmental sequelae of different patterns or orientations (styles) of attachment, including why each pattern or style should be "adaptive" in certain environments.

Even though each middle-level evolutionary theory addresses a specific set of adaptive problems, many of them have overlapping implications for social behavior. Kin selection theory, for example, also stipulates when conflict should arise between parents and their children; parent-offspring conflict theory specifies when reciprocal altruism should emerge between different sets of pair-bonded parents; and reciprocal altruism theory addresses when men and women might strive to attain status and ascend social hierarchies in groups (Simpson, 1999). In some cases, middle-level theories generate different hypotheses and predictions regarding a given outcome. For some phenomena, therefore, there is no single evolutionary prediction, particularly if competing middle-level theories are involved (Buss, 1995). What is most important to appreciate is that predictions derived from evolutionary theorizing *are* empirically testable.

Stable Features of the Social EEA

In order to understand the context in which the attachment system evolved and the problems it was designed to "solve," one must consider the physical and social environments that humans most likely inhabited during evolutionary history. Although attachment theorists have speculated about what the EEA may have been like (especially the physical EEA; see Bowlby, 1969/1982), less consideration has been given to the *social EEA* (Simpson & Belsky, 2008).

For most of our evolutionary history, humans were hunters and gatherers (Cronk, 1999; Kelly, 1995) who lived in small, cooperative groups (Brewer & Caporael, 2006; Eibl-Eibesfeldt, 1989). Most people within a tribe were biologically related to one another, and strangers were encountered rather infrequently, mainly during intertribal trading, social contact, or war (Wright, 1994). Though people occasionally migrated in and out of their natal groups, most remained in the same tribe their entire lives. Men and women formed long-term pair bonds (Cronk, 1999), but serial monogamy was probably most common (Fisher, 1992). Children were born approximately 4 years apart and were raised with considerable help from extended family and perhaps even non-kin (Wright, 1994); few children were raised exclusively by their biological parents. Humans, in fact, were probably “cooperative breeders” who shared childrearing with their kin (Hrdy, 1999, 2005). Younger children most likely spent considerable time being socialized by older children (Eibl-Eibesfeldt, 1989) if they survived premature death, especially during the first 5 years of life. Both men and women were involved in securing food, with men doing most of the hunting and women doing most of the gathering (Wood & Eagly, 2002). Participation in the daily functioning of small, cooperative groups may in fact have been the predominant survival strategy of early humans (Brewer & Caporael, 2006). These likely features of the social EEA must be considered when conceptualizing attachment theory within an evolutionary framework.

Normative and Individual-Difference Components of Attachment

As mentioned earlier, attachment theory has two primary components: (1) a normative component that explains modal or species-typical patterns and stages of attachment in humans (e.g., “How and why are attachment bonds formed?”), and (2) an individual-difference component that explains deviations from modal or normative patterns and stages (e.g., “How and why do different patterns of attachment exist?”). The attempt to account for both species-typical patterns of behavior and predictable individual differences is a hallmark of nearly all major middle-level evolutionary theories.

Normative Features of Attachment

There are three normative features of attachment that have especially important ties to evolutionary principles (Simpson & Belsky, 2008): the “synchronization” of infant–parent responses/behaviors during the first few months of life, young children’s need to maintain contact with and seek proximity to their caregivers, and the basic stages through which attachment propensities develop.

Synchronized Capabilities

Compared to most other species, human infants are born in an underdeveloped and premature state (Kaplan, Lancaster, & Hurtado, 2000). From the moment of birth, however, human infants are “prepared” to bond with their caregivers (Simpson, 1999), and several ways in which mothers behave—at birth and early in development—seem to operate in *synchrony* with the capabilities and limitations of their infants, facilitating infant–caregiver bonds (Simpson & Belsky, 2008). For example, mothers typically exaggerate their facial expressions, change them more slowly, and maintain visual contact for longer periods of time when interacting with infants than with others (Eibl-Eibesfeldt, 1989). When talking to infants, mothers engage in “motherese” (Fernald, 1985), slowing their speech, accentuating certain syllables, and speaking one octave above normal speech (Grieser & Kuhl, 1988). These patterns of behavior are preferred by most young infants and are well suited to their developing visual and auditory capacities. Systems that operate in a synchronous, lock-and-key fashion between codependent individuals, as those just highlighted do, are often a telltale sign of evolved adaptations.

Contact Maintenance and Proximity Seeking

According to Bowlby (1980), attachment behaviors include actions that promote proximity between children and their attachment figures. Young children engage in three classes of behavior to establish or maintain proximity to their caregivers (Bowlby, 1969/1982). *Signaling behaviors* (e.g., vocalizing, smiling) tend to draw caregivers toward the child, usually for positive interactions. *Aversive behaviors* (e.g., crying, screaming) bring caregivers to children, typically to terminate the aversive reactions. *Active behaviors* (e.g., ap-

proaching, following) move the child toward the caregiver. Though different phenotypically, these behaviors all serve the same evolutionary function—to keep vulnerable infants in close physical proximity to their caregivers, thereby increasing their chances of survival. Since death prior to reproduction was the first major threat to inclusive fitness, Bowlby reasoned that directional selection shaped the attachment system in humans, establishing the foundation of our social nature.

Phases of Development

According to Bowlby (1969/1982), attachment propensities develop through four phases in humans (see also Marvin, Britner, & Russell, Chapter 13, this volume). In the first phase, which takes place between birth and age 2–3 months, infants respond to a wide variety of social stimuli and people without exhibiting strong preferences for one attachment figure. Although Bowlby may have overestimated how open young infants are to contact comfort from multiple caregivers, he was correct in believing that infants are malleable in terms of whom they can and do bond with during the opening months of life. The early openness of the system may have facilitated survival—and may, therefore, have been selected—in a world where the risk of maternal death resulting from delivery and/or its complications was far more common than it is today.

During the second phase, which occurs between age 2–3 months and about 7 months, infants display greater discrimination in social responsiveness. They begin, for instance, to distinguish caregivers and family members from strangers, selectively prefer certain persons, and direct their attachment behaviors toward specific attachment figures. Such discrimination should have helped the infant “reel-in” the caregiver, further facilitating survival (in the service of eventual reproduction), and thus resulting in its selection.

In the third phase, which extends from age 7 months to roughly 3 years, children play a more active role in seeking proximity and initiating social contact. During this phase, they also start developing internal working models (i.e., beliefs, expectancies, and attitudes about relationships based on experiences with attachment figures) of themselves and significant others (Bowlby, 1973). This is also when the three primary “functions” of attachment are first seen in the child’s behavior: *proximity maintenance* (staying near to, and resist-

ing separations from, the attachment figure), *safe haven* (turning to the attachment figure for comfort and support), and *secure base* (using the attachment figure as a base from which to engage in nonattachment behaviors). If children in this phase have prolonged separations from their attachment figures, they experience the three stages of response to separation: protest, despair, and detachment. For reasons outlined earlier, these responses should also have aided and abetted survival and reproduction, thereby leading to their selection.

The fourth phase, which begins around age 3, marks the beginning of behaviors that signal goal-corrected partnerships with attachment figures. Given the further development of their language skills and theory-of-mind capabilities, children start to see the world from the perspective of their interaction partners. This allows them to incorporate the goals, plans, and desires of their partners into their own decision making, which results in the negotiation of joint plans and activities. These unique abilities should also have facilitated the formation and maintenance of pair bonds and, thus, may have been selected by evolutionary processes.

As children move through the toddler years, their desire for physical proximity is gradually replaced by a desire to maintain psychological proximity (i.e., felt security; Sroufe & Waters, 1977). Early in adolescence, overt manifestations of attachment bonds with parents subside, and the three functions of attachment—proximity maintenance, safe haven, and secure base—are gradually transferred from parents to peers and romantic partners as adolescents enter adulthood (Furman & Simon, 1999). During this final stage, the centrality of reproduction as an evolutionary process becomes more obvious and direct instead of indirect (i.e., through enhancing survival).

Individual Differences in Attachment

Although infants are biologically predisposed to form attachment bonds to their caregivers, the type of bonds they form ought to depend on the conditions in which they are raised, as Bowlby (1969/1982) and Ainsworth (1979) proposed. Perceptions of environmental conditions, in turn, should be filtered through evolved psychological mechanisms, including sensation (e.g., physical warmth), perception (e.g., caregiver responsiveness), and representations (e.g., internal working mod-

els). Such psychological mechanisms are typically activated by specific environmental cues, resulting in “optimal” ecologically contingent strategies that evolved to solve specific adaptive problems posed by certain kinds of environments (Buss, 1995; Tooby & Cosmides, 1992).¹

Infants, of course, do not have the cognitive ability to appraise the quality of local environmental conditions, such as whether the environment is safe, and plentiful and rich in resources versus threatening, harsh, and impoverished. However, they *do* have the ability, which is well appreciated by attachment theory, to determine whether caregivers are sensitive, responsive, and attentive to their biological needs. Such information ought to provide clues about the nature and quality of current—and perhaps future—environmental conditions (Belsky, 1997; Chisholm, 1996; Frankenhuis, Gergely, & Watson, 2013). If caregivers in evolutionary history were able to devote the time, effort, and energy necessary to be sensitive, responsive, and attentive to the needs of their children, the local environment was probably safe and sufficiently rich in resources, broadly defined. In contrast, if caregivers were insensitive, nonresponsive, and devoted less attention to their children, the local environment was probably less resource-rich and perhaps even dangerous.

Ainsworth’s Strange Situation is well suited to detect different patterns of attachment because it presents infants with two common cues to danger in the EEA: being left alone, and being left with a stranger. Examining reunions between mothers and their 12- to 18-month-old infants, Ainsworth, Blehar, Waters, and Wall (1978) identified three primary attachment patterns in young children: secure, anxious-ambivalent, and anxious-avoidant. Upon reunion, securely attached children use their caregivers to regulate and attenuate their distress, resuming other activities (e.g., exploration, play) rather quickly after calming down. Anxious-avoidant children retract from their caregivers upon reunion, opting to control and dissipate their negative affect in an independent, self-reliant manner. Anxious-ambivalent children make inconsistent and conflicted attempts to derive comfort and support from their caregivers, intermingling clinginess with outbursts of anger (see Fearon & Belsky, Chapter 14, and Solomon & George, Chapter 18, this volume).

Each attachment pattern reflects a different “strategy” that would have solved adaptive problems posed by different kinds of rearing environments (Belsky, 1997; Chisholm, 1996; Main,

1981). Mothers of securely attached infants tend to be available and responsive to the needs and signals of their infants (Ainsworth et al., 1978; De Wolff & Van IJzendoorn, 1997). Largely because of this, secure children do not have to worry about the availability and responsiveness of their caregivers, which allows them to concentrate on other life tasks.

Anxious-ambivalent children have caregivers who tend to behave inconsistently toward them (Ainsworth et al., 1978), sometimes because of poor or deficient parenting skills (Isabella, Belsky, & von Eye, 1989; Lewis & Feiring, 1989). Among children who are maltreated, anxious-ambivalent children are more likely to have been victims of parental neglect (Youngblade & Belsky, 1989). Thus, the demanding nature of anxious-ambivalent children may reflect an ecologically contingent strategy designed to obtain, retain, or improve greater parental attention and care (Cassidy & Berlin, 1994; Main & Solomon, 1990). For children with such parents, this behavioral strategy would have increased proximity to caregivers, solicited better care, and improved the child’s chances of survival (and eventually reproduction).

Avoidant children usually have caregivers who are cold and rejecting (Ainsworth et al., 1978). Among maltreated children, avoidant children are more likely to have suffered physical or emotional abuse from their parents (Youngblade & Belsky, 1989). The evolutionary origins of avoidance, however, may be more complex and multifaceted than those of anxious-ambivalence. Bowlby (1980) conjectured that avoidance allows infants to disregard cues that might activate the attachment system. If such cues were fully processed, avoidant infants might recognize the true inaccessibility and rejecting demeanor of their primary caregivers, which could be incapacitating.

Two additional evolutionary explanations for avoidance in childhood have been proposed. According to Main (1981), the distant, self-reliant behavior that characterizes avoidant infants enables them to maintain reasonably close proximity to belligerent or overwhelmed caregivers without driving them away. Avoidance, in other words, may have evolved to overcome deficiencies in caregiving provided by highly distressed, hostile, or unmotivated parents. During evolutionary history, this behavioral strategy would have increased the survival of infants who, if they put too many demands on their parents, might have been abandoned. Alternatively, earlier reproduction may

facilitate inclusive fitness in some circumstances, especially in harsh environments with few resources (Trivers, 1985). If maternal rejection was a valid proximal cue of the severity of future environments, avoidant tendencies might motivate children not only to move away from their parents earlier but also to become more opportunistic and risk taking, thereby facilitating survival and early reproduction in arduous environments (Belsky, 1997; Belsky et al., 1991). Moreover, if the stress experienced by insecure children undermined their health, internal bodily signals indicating declining health and increased morbidity or mortality may also have played a role in strategically regulating development (Belsky, 2014; Rickard, Frankenhuis, & Nettle, 2014).

As children enter adolescence, cumulative experiences in relationships are further assimilated into internal working models, which are continuously being updated and revised. These models reflect the degree to which individuals (1) believe they are worthy of love and affection, and (2) view significant others as loving and affectionate (Mikulincer & Shaver, 2007). Unlike in childhood, however, the attachment system in adulthood becomes integrated with the mating and caregiving systems (Shaver, Hazan, & Bradshaw, 1988), making adult attachment orientations (styles) more challenging to interpret than attachment patterns in children.

Attachment Theory and Parent–Offspring Conflict Theory

One middle-level evolutionary theory that has considerable relevance to attachment theory is parent–offspring conflict theory (Trivers, 1974). According to this theory, children (who share 50% of their genes with parents and full siblings) should want greater investment from their parents than their parents have been selected to provide. As a result, parents and offspring have slightly divergent reproductive interests, which result in conflict that peaks during the final stages of weaning. Stated another way, the evolutionary interests of parents and their infants are not perfectly aligned, which means that what is good for the child is not necessarily good for the parent, and vice versa. Unlike many current applications of attachment theory, the modern evolutionary perspective does not romanticize or idealize parent–child relationships.

Parent–Offspring Conflict Theory and Parental Investment

According to Trivers (1972), parental investment involves any actions performed by a parent for his or her offspring that increase the offspring's chances of survival, while reducing the parent's ability to invest in other current or future offspring. The level of investment depends on the costs and benefits associated with a given parental act or behavior. *Costs* are defined as units of forgone reproductive success by other current or future offspring, and *benefits* are defined as units of reproductive success of the current offspring (Trivers, 1974). In humans, acts of investment include allocating time, effort, energy, or resources to children through activities such as feeding, protecting, sheltering, and teaching. The amount of investment that children seek and parents offer should hinge on how both parties view the costs and benefits of different forms of parental investment.

When infants are young and highly dependent on their parents for care and resources, the costs of investment to parents are low and the benefits to infants are high from the reproductive standpoint of each party. During the early stages of childrearing, therefore, the reproductive interests of parents and their offspring coincide reasonably well, but not perfectly. However, as infants grow, consume more resources, and become more self-sufficient, the reproductive interests of parents and offspring diverge. From the parents' perspective, the costs of investment continue to rise over time while the benefits the infant derives from additional investment asymptotes. During this phase, directing investment to new offspring could enhance parents' reproductive success more than continuing to invest in an increasingly autonomous, self-sufficient child. This is the point at which weaning takes place in most cultures.

Given that children share only half of their genes with their parents and full siblings, two of their siblings must survive and successfully reproduce to propagate the infant's genes fully to future generations. Thus, infants should “devalue” the costs of investment incurred by their parents by 50%, expecting twice as many benefits as their parents have been selected to provide. Children and parents, therefore, should experience conflict until, from the perspective of the parent, the cost of parental investment is more than twice the benefit to the infant (or, from the perspective of the child, the cost of parental investment exceeds self-benefit). When this point is reached, the child's

inclusive fitness would be reduced if he or she continued to demand additional investment. Conflict should then subside as the child accepts the diversion of parental investment to other siblings.

Attachment theory does not fully recognize and account for the somewhat different reproductive interests of infants and their caregivers. Instead, scholars often assume that the evolutionary interests of parents and their children are largely equivalent and that, barring significant abnormalities, each child should be of equal “reproductive value” to its parents. Both of these assumptions are questionable. The reproductive value of a child should depend on several factors (Daly & Wilson, 1981; Trivers, 1974), including attributes of (1) the infant (e.g., his or her health, normality), (2) the mother (e.g., her health, age, ability to provide for the infant), (3) the father (e.g., the certainty of his paternity, his resources, his willingness to invest in the infant), (4) the nuclear family (e.g., the number of existing children, their birth spacing, the presence of stepsiblings), and (5) the local environment (e.g., whether or not resources are available to minimize the costs and maximize the benefits of further parental investment). When the costs of investing in a given child are disproportionately high relative to the benefits, parents should display preferential investment in certain children (Daly & Wilson, 1981). In some instances, attachment insecurity might arise from conditions that lower parental investment. Lower levels of investment should be evident in inadequate or poor caregiving behaviors, such as parental inattentiveness, neglect, rejection, abuse, and infanticide in extreme cases.

Cross-cultural research reveals that parental investment is, in fact, lower in families that have at least one biologically unrelated parent; when fathers question their paternity; when infants are ill, weak, or deformed, during periods of famine; when families are poor or lack social support; when mothers are very young; when families have too many children; and when birth spacing is too short (Daly & Wilson, 1988; Hrdy, 1999).

Parental Investment and Attachment

Relatively little is known about whether the conditions that reduce parental investment actually *cause* insecure attachment in children, primarily because it is unethical to employ such experimental interventions. However, strong links have been chronicled between certain contextual factors and

the quality of parental care, which is causally related to attachment security (Fearon & Belsky, Chapter 14, this volume). These factors include parental psychological health and well-being (e.g., Belsky & Jaffee, 2006), quality of marital/romantic partner relations (e.g., Krishnakumar & Buehler, 2000), and social support/connectedness (e.g., Andresen & Telleen, 1992). This research indicates that the greater the well-being, marital quality, and social support, the more sensitive, responsive, stimulating, and less detached (or hostile) the parenting tends to be. These “determinants of parenting” (Belsky, 1984) are also related to attachment security in the expected direction, such that better conditions instill greater security, which fosters better parental well-being (e.g., Atkinson et al., 2000; Jacobson & Frye, 1991). There is even evidence that parenting is the proximate mediator linking these more distal contextual factors with attachment security (e.g., Crittenden, 1985).

Evolutionary Models of Social Development across the Lifespan

Attachment theory addresses social and personality development “from the cradle to the grave” (Bowlby, 1979, p. 129). Most early attachment research, however, investigated certain barriers to inclusive fitness (e.g., problems associated with infant survival) to the relative exclusion of other barriers (e.g., problems associated with mating and reproduction). Even though some early attachment theorists (e.g., Main, 1981) conjectured that different attachment patterns in children might reflect different evolved strategies for promoting survival under certain rearing conditions, childhood attachment patterns were not theoretically tied to the development of different adult romantic attachment styles and mating orientations until the early 1990s, when Belsky and his colleagues (1991) published an influential paper on human social development from an evolutionary/attachment perspective.

Life History Theory

More recent theoretical developments have been guided by life history theory (LHT) (Charnov, 1993). LHT addresses how and why individuals allocate time, energy, and resources to different traits, behaviors, and life tasks when they are faced with tradeoff decisions that could influence their

reproductive fitness (Kaplan & Gangestad, 2005). In particular, LHT models the selection pressures in our ancestral past that should have determined when, and the conditions under which, individuals allocated time, energy, and resources to physical development, growth, reproduction, body repair, or aging.

According to most life history models, individuals can increase their reproductive fitness in two general ways (Parker & Maynard Smith, 1991). First, they can “invest” in traits or attributes that affect the timing of their mortality (i.e., the age at which they die). Second, they can “invest” in traits or attributes that influence the timing of their fertility (i.e., the age and rate at which they reproduce). Many life history traits/attributes, however, have countervailing effects on mortality and fertility (Kaplan & Gangestad, 2005). Traits or attributes that improve fertility through more frequent or more intense mating effort, for example, usually shorten survival, because many of the traits that make people (particularly men) more attractive to the opposite sex compromise the immune system (Grafen, 1990). Moreover, the allocation of energy and resources to growth during development tends to retard fertility when individuals are young, but enhance it once individuals mature sexually (Charnov, 1993). And the allocation of time, energy, and resources needed to ensure that one’s children grow to be strong and healthy typically undermines one’s own future fertility and survival.

Because one “can’t have it all,” individuals must negotiate three fundamental tradeoffs during their lives: (1) whether to invest in present (immediate) reproduction or future (delayed) reproduction; (2) whether to invest in higher quantity or higher quality offspring; and (3) whether to invest in mating effort or parenting effort. The way in which each tradeoff is resolved ought to depend on several factors, including the demands of the local environment (e.g., how taxing it is, the number of pathogens it contains, whether biparental care is required); the health, skills, abilities, and resources available to an individual at that time; the health, skills, abilities, and resources of others (e.g., kin, potential mates, competitors); and so forth.

The Belsky, Steinberg, and Draper Model

Inspired by LHT and earlier research on father absence during childhood (Draper & Harpending, 1982), Belsky and colleagues (1991) developed the first evolution-based and attachment-oriented

lifespan model of human social development. According to this model, the main evolutionary function of early social experience is to “prepare” children for the social and physical environments they are likely to encounter during their lifetime. The model focuses primarily on rate of development (i.e., faster vs. slower) and therefore offspring quantity versus quality tradeoffs. Ellis (2004) has labeled it “psychosocial acceleration theory” even though the theory addresses both slower and faster development. Certain information gleaned from the early environment should allow individuals to adopt an appropriate reproductive strategy—one that, on average, best increases inclusive fitness—in future environments. Hinde (1986), for example, proposed that if maternal rejection is induced by harsh environments in which competition for limited resources is intense, offspring who are aggressive and noncooperative should have higher reproductive fitness as adults than those who do not display these attributes. Conversely, offspring raised in environments with abundant resources could increase their fitness by adopting a more cooperative and communal orientation in adulthood.

The five-stage Belsky and colleagues (1991) model proposes that (1) early contextual factors in and around the family of origin (e.g., level of stress, spousal harmony, financial resources) affect (2) early childrearing experiences (e.g., level of sensitive, supportive, and responsive caregiving). These experiences then affect (3) psychological and behavioral development (e.g., attachment patterns, internal working models) that in turn influence (4) somatic development (i.e., how quickly sexual maturation is reached) and eventually (5) the adoption of specific ways of mating and parenting. These stages are linked sequentially, but earlier stages may statistically interact to predict later outcomes. Early contextual factors in the family of origin, for instance, can interact with early childrearing experiences to forecast the rate of somatic development.

Belsky and colleagues (1991) hypothesized that two developmental trajectories culminate in two reproductive strategies in adulthood (although they could also be opposite ends of a single continuum rather than discrete vs. continuous phenotypes). One strategy entails a short-term, opportunistic orientation toward close relationships, especially with regard to mating and parenting, in which sexual intercourse occurs earlier in life, romantic pair bonds are short-lived and less stable, and parental investment is lower. This orientation is geared to increase the *quantity* of off-

spring. The second strategy entails a long-term, investing orientation toward mating relationships in which sexual intercourse occurs later in life, romantic pair bonds are stronger and more enduring, and parental investment is greater. This orientation maximizes offspring *quality*. A critical and novel prediction derived from this model involving rate of development is that early rearing experiences should influence the timing of puberty. Specifically, sexual maturation should occur earlier for individuals who develop along the “quantity trajectory” than for those who develop along the “quality trajectory.”

A large body of evidence supports the Belsky and colleagues model (for reviews, see Belsky, 2012; Ellis, 2004; Simpson & Belsky, 2008). For example, consistent with nonevolutionary perspectives, greater socioemotional stress in families is associated with more insensitive, harsh, rejecting, inconsistent, and unpredictable parenting practices. Economic hardship (McLoyd, 1990), occupational stress (Bronfenbrenner & Crouter, 1982), marital discord (Belsky, 1981; Emery, 1988), and psychological distress (McLoyd, 1990) are all precursors of more hostile and/or detached parenting styles. Conversely, greater social support and more economic resources facilitate warmer and more sensitive childrearing practices (Lempers, Clark-Lempers, & Simons, 1989), perhaps because less taxed parents are more patient with or tolerant of their young children (Belsky, 1984).

The link between parental sensitivity and the psychological and behavioral development of children is also well established, consistent with both attachment theory and many other theories (e.g., social learning, emotion socialization, life course). During the first year of life, insensitive and unresponsive caregiving predicts the development of insecure attachments (De Wolff & Van IJzendoorn, 1997), which in turn forecasts behavior problems later in development. Insecurely attached 2-year-olds, for instance, are less tolerant of frustration (Matas, Arend, & Sroufe, 1978). Insecurely attached preschoolers are more socially withdrawn (Waters, Wippman, & Sroufe, 1979), less likely to display sympathy to distressed peers (Waters et al., 1979), less willing to interact with friendly adults (Lutkenhaus, Grossmann, & Grossman, 1985), and less well liked by their classmates (LaFreniere & Sroufe, 1985). During elementary school, insecure children have more severe behavior problems, especially aggression and disobedience (Lewis, Fiering, McGuffog, & Jaskir, 1984). According to Belsky and colleagues (1991), these

behaviors are governed by insecure working models, which prepare the child for opportunistic advantage taking and, therefore, noncommunal relationships later in life.

The most novel part of the model concerns what predicts the rate of somatic development. Belsky and colleagues (1991) hypothesized that children exposed to greater socioemotional stress develop insecure attachments, exhibit behavior disorders, and should reach puberty—and thus reproductive capacity—earlier than children without these attributes. According to life history logic (Chisholm, 1993, 1999; Kaplan & Gangestad, 2005), environments in which resources are scarce, relationship ties are tenuous, and mortality risks are elevated should cause more energy and effort to be allocated to rapid physical development, early mating, and short-term romantic pair bonds. This developmental strategy should increase the chances of reproducing before dying (or should have done so in our ancestral past). On the other hand, environments in which resources are plentiful and relationship ties are reciprocal and enduring should lead to effort being channeled to further somatic development, later sexual maturity, delayed mating, and longer-term romantic pair bonds that contribute to greater parental investment. In more benign environments, reproductive fitness could be enhanced by deferring reproduction until (1) individuals have acquired the skills and resources needed to maximize the quality of each offspring, and (2) offspring can benefit from all of the embodied capital that humans need to reproduce successfully.

Several strands of evidence support these predictions (Belsky, 2012). First, greater parent–child warmth, cohesion, and positivity predict delayed pubertal development in both prospective longitudinal studies (Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999; Graber, Brooks-Gunn, & Warren, 1995) and retrospective or concurrent ones (Kim, Smith, & Palermi, 1997; Miller & Pasta, 2000). Second, greater parent–child conflict and coercion predict earlier pubertal timing in both prospective longitudinal studies (Ellis & Essex, 2007; Moffitt, Caspi, Belsky, & Silva, 1992) and retrospective or concurrent ones (Kim et al., 1997). Third, the happier and/or less conflict-ridden the parental relationship, the later pubertal maturation occurs in girls, both in prospective longitudinal studies (Ellis et al., 1999; Ellis & Garber, 2000) and in nonprospective ones (Kim et al., 1997). Indeed, early insecure attachment—measured at age 15 months—forecasts earlier age

of menarche and both onset and completion of pubertal development (Belsky, Houts, & Fearon, 2010). These results cannot be easily explained by traditional attachment theory, but they are central to psychosocial acceleration theory. Not all studies have found puberty-related links like those just highlighted. Steinberg (1988), for instance, did not find associations between the amount of family conflict/coercion and pubertal timing in girls. However, family experience–pubertal developmental links consistent with psychosocial acceleration theory have recently emerged in studies that take into account genetic confounding, either via sibling designs (Tithers & Ellis, 2008) or natural experiments (Pesonen et al., 2008).

Almost all of these findings are based on studies involving girls. Although it was once thought that this gender disparity could be attributable to the greater difficulty of measuring puberty in males, this fact does not seem to explain these sex differences. New theorizing by James, Ellis, Schlomer, and Garber (2012) has noted that the early versus later reproduction tradeoff central to Belsky and colleagues' (1991) original theorizing is more pressing for females, whereas that between somatic development and reproduction is more pressing for males, who must engage in considerable intrasexual competition for mates. Recent empirical work by this team provides evidence consistent with this important insight (James et al., 2012).

Evidence relevant to the final stages of the Belsky and colleagues (1991) model (i.e., the mating strategies individuals adopt in adulthood) comes from two sources: (1) research linking adult attachment styles to mating and romantic relationship functioning, and (2) research bridging adult attachment and parenting practices. Individuals who report being more securely attached to romantic partners are less likely to have promiscuous sexual attitudes or engage in extrapair sex (Brennan & Shaver, 1995); are more likely to desire only one sexual partner over a 30-year period (Miller & Fishkin, 1997); and, if female, have sexual intercourse at a later age than their insecure counterparts (Bogaert & Sadava, 2002). Securely attached adults also have more satisfying romantic relationships (J. Feeney, Chapter 21, this volume), display less negative affect and more constructive conflict resolution tactics when interacting with romantic partners (Simpson, Rholes, & Phillips, 1996), and engage in more self-disclosure and prove more responsive to self-disclosures by partners (Mikulincer & Nachson, 1991). Conse-

quently, secure adults are also less likely to divorce or separate (J. Feeney, Chapter 21, this volume), have longer lasting romantic relationships (Hazan & Shaver, 1987), and report greater commitment to and trust in their dating partners (Simpson, 1990) and spouses (Fuller & Fincham, 1995).

These findings, although consistent with Belsky and colleagues' (1991) original model, are limited due to their cross-sectional nature and their focus on romantic (rather than childhood) attachment assessments. Recent longitudinal research using data from the Minnesota Longitudinal Study of Risk and Adaptation has provided even more direct support for the model (see Simpson, Collins, & Salvatore, 2011). Simpson, Collins, Tran, and Haydon (2007), for example, have documented links between attachment security (assessed in the Strange Situation at 12 months) and how individuals experience and express conflict with their romantic partners 20 years later. Specifically, individuals classified as insecure at age 1 tend to experience and express relatively more negative emotions in their romantic relationships in their early 20s, and this effect appears to be mediated through their lower social competence in grade school and their less secure same-sex friendships at age 16.

Supporting the Belsky and colleagues (1991) model, adult attachment is also associated with differential expectations about children and parenting even before individuals have children. Rholes, Simpson, Blakely, Lanigan, and Allen (1997), for instance, found that insecurely attached college students anticipate being more easily aggravated by their young children if/when they become parents, expect to be more strict disciplinarians, believe they will express less warmth toward their children, and are less confident about their ability to relate well to them. In addition, avoidant college students believe they will derive less satisfaction from caring for their young children and express less interest in having them. Once they have children, avoidant parents report feeling less emotionally close to their first newborn child as soon as 2 weeks after birth (Wilson, Rholes, Simpson, & Tran, 2007), and avoidant mothers are less emotionally supportive of their preschooler children, adopting a detached, controlling, or instrumentally focused mode of relating to them (Crowell & Feldman, 1991; Rholes, Simpson, & Blakely, 1995). (For a review of studies of self-reported adult attachment patterns and parenting characteristics, see Jones, Cassidy, & Shaver, 2015.)

Furthermore, mothers classified as secure on the Adult Attachment Interview (AAI) (who in many cases received greater warmth and contingent care from their own parents) are more sensitive to and supportive of the needs of their children (Hesse, 2008, Chapter 26, this volume; Van IJzendoorn, 1995). For example, attachment security is linked with greater warmth and more appropriate structuring of learning tasks by fathers and mothers (Adam, Gunnar, & Tanaka, 2004), greater emotional support in various situations (Crowell & Feldman, 1991), less negativity (Slade, Belsky, Aber, & Phelps, 1999), and greater awareness of the child's needs (Das Eiden, Teti, & Corns, 1995).

The Chisholm Model

Chisholm (1993, 1996) extended Belsky and colleagues' (1991) thinking by proposing a slightly revised and expanded model of alternative reproductive strategies, one that focuses on the immediate versus delayed reproduction life history tradeoff. This work advanced our thinking in three significant ways. First, it drew attention to local mortality rates as being the critical cues that humans monitor to regulate their rate of development and, ultimately, their reproductive strategies. After all, high mortality rates ought to have been a direct barometer of the difficulty of local environments, and they should have been associated with poorer caregiving in the EEA. According to Chisholm (1993, 1996), parental indifference or insensitivity—being a valid cue of local mortality rates—would have motivated children to develop avoidant working models and behaviors that should have increased fitness in such arduous environments. Low mortality rates, which should have signaled more hospitable environments, should have been associated with better and more attentive caregiving. Sensitive parenting, in other words, should have conveyed to children that premature death was less likely, resulting in secure working models and behaviors that enhanced fitness in benign environments.

Consistent with Chisholm's theorizing is evidence connecting adverse life conditions with expectations regarding longevity and the timing of reproduction later in life (Nettle, 2010; Nettle & Cockerill, 2010). For example, as life expectancy declines in a local area, the probability of women reproducing by age 30 increases (Wilson & Daly, 1997), and teen mothers who expect to die at a younger age are more likely to become mothers

at an earlier age (Johns, 2003). Such findings are consistent with Geronimus's (1996) "weathering hypothesis," which states that early birth is a strategic response to the rapid decline in health among women, especially poor women, in their 30s and 40s. This underscores the value of treating local mortality rates as a powerful cue in the development of alternative reproductive strategies.

Besides highlighting the importance of local mortality rates, Chisholm (1999) also called attention to *time preference*—the tendency to discount the future by favoring smaller, immediate rewards over larger, delayed ones—as the psychological mechanism linking early rearing experiences with the timing of future mating and parenting behavior. Individuals raised in harsh or unpredictable (i.e., insecurity-inducing) environments, in which waiting for rewards could result in leaving no descendants, ought to prefer immediate payoffs, even if delayed ones might be significantly better (Wilson & Daly, 2005).

Chisholm's (1996) third major contribution was his identification of two parent-based threats to the survival and growth of children in the EEA—parents' *inability* and *unwillingness* to invest in offspring—to which children should have evolved to detect and respond. Thus, the secure attachment pattern is a facultative adaptation to parents' ability and willingness to provide high investment, as reflected in their warm/sensitive caregiving. The avoidant attachment pattern, in contrast, is an adaptation to parents' unwillingness to invest (regardless of their ability), reflected in their cold/rejecting caregiving. Finally, the anxious-ambivalent pattern is an adaptation to parents' inability to invest, reflected in their inconsistent/unpredictable caregiving.

The Belsky and colleagues and Chisholm models have both played important roles in getting scholars to think more deeply about how and especially *why* early experiences shape subsequent development, something that many developmental psychologists have simply taken for granted. Both models, however, have been expanded and further refined by the infusion of additional evolutionary considerations. First, neither model addresses all of the factors that, from an evolutionary standpoint, should govern the adoption of specific reproductive strategies in adulthood. Mate selection is contingent on a multitude of factors, ranging from a potential mate's genetic quality to his or her ability to accrue and share resources, to his or her capacity to impart knowledge and information to offspring (Gangestad & Simpson, 2000).

In addition, psychosocial acceleration theory, as originally conceptualized, was not sufficiently sensitive to the different roles that men and women assume in reproduction (Buss & Schmitt, 1993; Geary, 2005). This inspired James and colleagues (2012) and Del Giudice (2009) to develop sex-differentiated models that accentuate the different life history tradeoffs that females and males must negotiate. For females, the critical tradeoff is between early and later reproduction; for males, it is between growth and reproduction. Despite these limitations, the Belsky and colleagues and Chisholm models represent important advances in our understanding of attachment and social development across the lifespan.

The Del Giudice Model

Del Giudice (2009) has developed a model that incorporates sex differences within an explicitly attachment/evolutionary framework and, in so doing, extends psychosocial acceleration theory in some novel ways. Recent cross-cultural research indicates that boys are more likely to be avoidantly attached in middle childhood, whereas girls tend to be anxious (reviewed in Del Giudice, 2009; for an alternative view, see Van IJzendoorn & Bakermans-Kranenburg, 2010). Del Giudice argues that sex differences in attachment patterns in middle childhood might have adaptive significance for both children and adults because they reflect the enactment of sex-specific life history strategies. Consistent with Belsky and colleagues (1991), early psychosocial stress and insecure attachment patterns are viewed as cues of heightened environmental risk, which shift development toward reproductive strategies that facilitate current reproduction over later reproduction and emphasize mating effort over parenting effort. In line with well-established sex differences between mating and parenting effort (Geary, 2005), insecure males typically enact avoidant strategies, whereas insecure females enact anxious ones, both of which increase subsequent investment from kin and mates. (Females ought to become avoidant, however, when environmental risks become high.)

The most novel part of the model is the proposal that sex differences in attachment should emerge in middle childhood—for reproductive-fitness-related reasons—rather than occurring earlier in development, which is the focus of psychosocial acceleration theory. Indeed, adrenarche (the early stages of sexual maturation) is theorized

to be a “developmental switch-point,” reorganizing attachment during middle childhood, which then has several important implications for ties between attachment patterns and sexual development across the lifespan. Specifically, at the start of middle childhood, insecure children’s attachment patterns become sex-biased, shunting reproductive strategies down sex-optimal developmental pathways. Because attachment security versus insecurity early in childhood is a good barometer of local ecological risk, it has been retained by evolution as a stable, prototype-like behavioral trait (Fraley, 2002). These early strategies, however, are disposable phenotypes that can be modified later in development if they no longer match the environmental demands to which the developing child is exposed. This is important, Del Giudice (2009) claims, because avoidant and anxious attachment patterns have different adaptive value for boys and girls with regard to competition in same-sex peer groups in middle childhood.

According to Del Giudice (2009), the strongest selection pressure on attachment patterns in middle childhood should come from intrasexual competition within peer groups when children start competing with others for status, attention, and resources. Negotiations within these groups should be particularly challenging for insecurely attached children, who can no longer count on their nuclear family members to buffer them from all the inherent stress and failures. The avoidant behavioral pattern, which is characterized by heightened aggression, excessive self-reliance, and inflated self-esteem, is used more effectively by males to attain higher status and popularity in middle childhood peer groups (Benenson, 2014). Girls, in contrast, shift to anxious patterns that help them utilize “tend-and-befriend” tactics (Taylor et al., 2000), which are more effective at promoting ascension and success within their social groups.

Successful social strategies, of course, do not always involve competitive status seeking. If environmental conditions are safe/predictable, and monogamy and high paternal investment define the local mating system, low-risk, cooperative strategies ought to maximize males’ long-term fitness better, with less male avoidance (i.e., greater security) resulting in less male–male competition and lower conflicts of interest between mothers and fathers.

Maternal and paternal attachment might also differentially affect the behavioral strategies that children adopt in middle childhood. Mater-

nal and paternal investments are differentially responsive to extrinsic risk (Quinlan, 2007), which could alter children's life history strategies in novel ways. The level of paternal investment, for instance, often contains more diagnostic information about the amount of male–male competition, polygyny, and paternal involvement within the local environment, which could shape children's levels of competitiveness and risk taking (especially in boys), as well as the adoption of avoidant versus anxious attachment patterns (particularly in girls). Future research needs to test these hypotheses and determine whether genotypic variability also affects the regulation of these life history-related traits.

The Ellis Model

Whereas psychosocial acceleration theory called attention to family dynamics, including marital and parent–child relational experiences in regulating the development of reproductive strategies (Belsky et al., 1991), Ellis and colleagues (1999; Ellis & Garber, 2000) drew upon Draper and Harpending's (1982) focus on father absence and Trivers's (1972) parental investment theory to hypothesize that fathers have a special role in the development of girls' reproductive strategies. Belsky and colleagues (1991) viewed early father absence as a marker of stress in the family of origin and appreciated the influence of the quality of both mothering and fathering. Ellis (2004), on the other hand, suggests that father absence or stepfather presence is a particularly salient, evolutionarily privileged cue of paternal investment that signals low, unpredictable, or changing levels of paternal investment in families.

Father absence does, in fact, predict accelerated pubertal development among girls, both in prospective studies in which girls are followed from childhood into adolescence (e.g., Campbell & Udry, 1995; Ellis & Garber, 2000; Ellis et al., 1999) and in retrospective studies of adults (e.g., Doughty & Rodgers, 2000; Hoier, 2003; Quinlan, 2003). Similar effects, however, have not been found in African American samples (e.g., Campbell & Udry, 1995; Rowe, 2000). In addition, research does not always find greater predictive power of fathering or the father–child relationship over mothering and the mother–child relationship (e.g., Ellis, Shirtcliff, Boyce, Dearthoff, & Essex, 2011). All too often, evidence of father effects on pubertal development comes from studies that

do not include measures of mothers (see Belsky, 2012).

Nevertheless, research does indicate that the earlier father absence occurs in a child's life (especially within the first 5 years), the more strongly it predicts the speed of female pubertal development (e.g., Ellis & Garber, 2000; Quinlan, 2003). Stepfather presence may also affect pubertal timing, perhaps accounting for some of the father absence effects (Ellis, 2004). Supporting this view, greater conflict between the mother and stepfather combined with earlier stepfather presence in the home is especially influential in accelerating pubertal development in girls (Ellis & Garber, 2000). Consistent with Belsky and colleagues' (1991) emphasis on the quality of parent–child relationships, Ellis and colleagues (1999) also found that girls' pubertal development is delayed the more time fathers spend caring for their daughters during the first 5 years of life and the more fathers have positive/affectionate interactions with their daughters at age 5.

Thus, there are good theoretical and even empirical grounds for *not* treating mothers and fathers as interchangeable agents of influence in understanding how childhood experiences shape reproductive strategies. Greater attention should be paid to the presence of biologically unrelated male figures in the home during development and to the differential influence of maternal and paternal investment (i.e., quality of parenting).

The Hazan–Zeifman and Kirkpatrick Models

Scholars have also attempted to explain the nature and strength of adult romantic pair bonds from a life history/attachment perspective. Hazan and Zeifman (1999; Zeifman & Hazan, 2008), for example, propose that adult romantic relationships are an instantiation of attachment relationships formed earlier in life. They point out many similarities between childhood attachment to caregivers and adult attachment to close peers and romantic partners (also see Shaver et al., 1988). Both infants and adults, for example, display similar reactions to separation from or loss of their attachment figures. In addition, people value qualities in prospective mates that parallel those they valued in their caregivers, and children and adults behave similarly when seeking close contact, physical intimacy, and affection from their attachment figures. Parent–child and adult–adult attach-

ment relationships also pass through a similar set of developmental stages.

Hazan and Zeifman (1999) suggest that the primary evolutionary function of secure attachment in adult relationships is to increase the likelihood of stable and enduring pair bonds so mates can provide better mutual support (see also Zeifman & Hazan, Chapter 20, this volume). Pair bonding, therefore, is conjectured to enhance the reproductive fitness of both parents and their offspring. Adult mating strategies are, in fact, related to the pair-bond status of one's parents, with father absence and greater marital discord in the family of origin predicting earlier sexual maturation, short-term mating strategies in adulthood, and less stable marriages (Belsky, 1999). Children who have more pair-bonded parents, by comparison, should adopt long-term mating strategies and emphasize quality rather than quantity of investment when they have their own children (Hazan & Zeifman, 1999). (See the earlier evidence linking positive marital and partner relationships with more supportive parenting and greater likelihood of having secure offspring.) More strongly pair-bonded partners should also contribute to their own reproductive success by providing each other with greater support, which is associated with better long-term physical and mental health and more regular ovulation patterns (Zeifman & Hazan, 1997).

Partially in response to this model, Kirkpatrick (1998) claims that adult attachment styles evolved to enhance reproductive fitness based on early childhood experiences but he questions whether security and protection are the *primary* functions of adult attachment. Instead, Kirkpatrick suggests that components of the caregiving system (e.g., love) may have been co-opted during evolutionary history to cement romantic pair bonds in adulthood, and that—similar to the views of Belsky and colleagues and Chisholm—adult attachment styles primarily reflect evolved reproductive strategies.

One of the principal life history tradeoffs involves allocating time and energy to mating effort versus parenting effort. Kirkpatrick (1998) argued that it was not always adaptive or advantageous for women and men to enact long-term, monogamous mating strategies (see also Gangestad & Simpson, 2000). Consequently, adult attachment styles may be a “mechanism” for choosing the best mating strategy given the nature of one's early childhood experiences and the quality of early parental investment. Individuals who receive consistently sensitive and responsive parenting should

develop secure working models, resulting in the adoption of long-term, committed mating strategies. These individuals should also develop greater trust and intimacy in their relationships (Simpson, 1990) and should fall in love with partners who have higher mate value (Hazan & Shaver, 1987), which they do. Avoidant individuals, in contrast, should have less committed relationships, pursue short-term mating strategies, and have more unrestricted sociosexual orientations, which they do (Simpson, Wilson, & Winterheld, 2004). And anxious persons should desire and want to pursue long-term mating strategies, yet their strong desire to be attractive to and merge with their romantic partners ought to result in short-term sexual relationships that are unstable (Kirkpatrick, 1998). Given these findings, Kirkpatrick (1998) believes that features of the caregiving system—especially love operating as a “commitment device” (Frank, 1988)—could have been co-opted to bind and stabilize long-term romantic pair bonds.

Conceptualizing the Early Developmental Environment

According to life history thinking, the quality of the environment early in life can exert long-lasting effects on psychosocial development, including the development of specific mating and parenting strategies in both males and females, and different rates of pubertal timing in females. In conceptualizing the early rearing environment, Ainsworth and her colleagues (1978) have identified sensitive responsiveness as a key factor regulating the development of secure versus insecure attachment patterns. Moreover, Chisholm (1996, 1999) has suggested that because parenting quality is a good barometer of local mortality rates, it serves as a powerful, evolved cue that shapes the development of secure versus insecure attachment patterns and, therefore, the development of slow versus fast reproductive strategies in adulthood.

These observations become especially interesting in light of a recent cross-species analysis by Ellis, Figueredo, Brumbach, and Schlomer (2009), who examined the environmental factors that regulate the development of different reproductive strategies in assorted species and made a critical distinction between exposure to harsh versus exposure to unpredictable environments early in life. Security, of course, emanates from warm, sensitive, and consistently responsive caregiving, whereas

insecurity stems from cold, insensitive, and inconsistent (or unpredictable) caregiving.

From a cross-species perspective, *harshness* refers to age-specific rates of morbidity–mortality in the local environment. In Western societies, harshness is indexed by socioeconomic status (SES), given that lower levels of SES are linearly related to nearly all forms of morbidity and mortality (Ellis et al., 2009). And, of course, such distal contextual conditions are associated with harsher, less supportive, and less responsive parenting (McLoyd, 1998). The harsher and poorer the environment, the higher the rate of morbidity (e.g., illness, injury) and mortality (death) at every age in a society. *Unpredictability* refers to stochastic changes (fluctuations) in the harshness of environmental conditions across time and may therefore incorporate inconsistent or unpredictable parenting. Unpredictability is signaled by important changes in the ecology of the family that directly affect parents and/or their children, such as frequent changes in the job status of parents, residential changes, and parental transitions such as divorce and remarriage (see Belsky, Schlomer, & Ellis, 2012; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012). Although a great deal of research by developmentalists studying attachment has unwittingly blended the two dimensions—especially at the proximate level when operationalizing sensitive parenting—Ellis and colleagues' (2009) model suggests that harshness and unpredictability might have independent effects on life history-relevant behaviors in young adulthood. However, this model does not delineate when each form of stress ought to forecast specific life history traits in adolescence or adulthood, and it does not speak to the origins of attachment security.

To date, only a few prospective longitudinal studies have tested the effects of environmental unpredictability and harshness in childhood on later behavior in direct response to Ellis and colleagues' (2009) theorizing. Brumbach, Figueredo, and Ellis (2009) found that exposure to both greater environmental unpredictability and harshness measured in adolescence independently predicted faster life history strategies in adolescence, such as engaging in more deviant social behavior. Belsky and colleagues (2012) observed that being raised in more unpredictable environments during the first 5 years of life forecasted having more sexual partners by age 15, both directly and as mediated by maternal depressive symptoms and maternal sensitivity (which were also assessed during childhood). Simpson and colleagues (2012)

reported that individuals exposed to less predictable environments between ages 0 and 5 displayed a faster life history strategy at age 23, having more sexual partners, engaging in more aggressive and delinquent behaviors, and being associated with criminal activities. Exposure to either harsh environments or experiencing unpredictability in later childhood (ages 6–16), however, did not predict these outcomes. Viewed together, these findings indicate that unpredictable childhood environments exert unique effects on risky behavior later in life, consistent with adopting a faster life history strategy, and there may be a developmentally sensitive window for assessing unpredictability. They also raise intriguing questions about whether one can distinguish harsh versus warm parenting from consistent/predictable versus inconsistent/unpredictable parenting when examining the interactional origins of attachment patterns.

A recent longitudinal study has investigated the effects of early unpredictability on parenting 30 years later. Using data from the Minnesota Longitudinal Study of Risk and Adaptation, Szepeswol, Simpson, Griskevicius, and Raby (in press) found that for males, exposure to greater unpredictability during the first 5 years of life forecasts less parental involvement/investment and less supportive parenting behavior in men who have children. These effects, however, were mediated through the quality of care that mothers gave their male children and the attachment representations of childhood that these males harbored in adulthood. Specifically, males (but not females) exposed to greater unpredictability during the first 5 years of life had mothers who were rated by observers as providing less sensitive care/support (i.e., less predictable warmth) between years 0 and 5, which in turn predicted them having more insecure attachment representations at age 26 (assessed by the AAI). Age 26 AAI insecurity, in turn, forecasted less observer-rated parental involvement/investment as well as less supportive behavior in adulthood. This evidence is important because it links unpredictability to actual parenting behavior, which is a critical component of Belsky and colleagues' (1991) original model.

Unresolved Issues, Promising Directions, and Conclusions

We have covered only a few of the several unresolved issues and promising directions for future

research. Two of the most perplexing questions center on why maternal sensitivity accounts for only a portion of the variance in children's attachment status and why the intergenerational transmission of attachment patterns is not stronger than it is (Van IJzendoorn & Bakermans-Kranenburg, 1997). LHT might be able to provide solutions to these puzzles.

Applying evolutionary bet-hedging logic, Belsky (1997; Belsky & Pluess, 2009) and Boyce and Ellis (2005; Ellis, Boyce, Belsky, Bakermans-Kranenburg, & Van IJzendoorn, 2011) have theorized that children should differ in their susceptibility to parental influence. Belsky and his colleagues suggest that differential susceptibility could be adaptive for parents, children, and their siblings if a parent's attempt to "prepare" his or her children for the future environment is mistaken due to the inherent unpredictability of future conditions. This would explain why, from an evolutionary standpoint, differential susceptibility to parental influence is witnessed within families. It would also explain why intergenerational transmission effects are weaker than expected. There is even more evidence, both observational and experimental, that children vary in their susceptibility to parenting and other influences (Belsky & Pluess, 2009, 2013). Most notable is discovery of a recent gene \times environment interaction by Manuck, Craig, Flory, Halder, and Ferrell (2011), which indicates that the theory-distinguishing prediction of psychosocial acceleration theory—that exposure to an adverse rearing environment predicts earlier sexual maturation—holds for girls who carry one version of estrogen receptor genes but not another. Given that most attachment-related research is still not informed by a differential-susceptibility perspective, past research may have both under- and overestimated certain effects of rearing experiences on attachment outcomes—underestimated for those individuals who are more susceptible, and overestimated for those who are less susceptible.

If the early rearing environment regulates the development of reproductive strategies, which now seems likely, we need to determine exactly *how* certain environmental cues actually shape attachment patterns and reproductive strategies. Frankenhuis and Panchanathan (2011) have proposed that among those who are more susceptible to environmental regulation, the timing of "commitment" to a particular course of development (e.g., secure attachment, slower physical development) may depend on the clarity of the contextual

cues. When cues are clear and consistent, a "reading" of them may lead to earlier commitment, but when they are less clear or when more time is required to decipher the environmental "tea leaves," individuals may defer commitment to one developmental pathway versus another. Attachment and developmental theorists should contemplate the implications of this possibility. Might some children who appear insecure early in life but then develop secure representations have experienced less consistent sensitive caregiving cues and, therefore, required more time before "committing" to such a developmental pathway? If so, could this explain why the presumed developmental antecedents of early attachment patterns are neither as strong nor as reliable as attachment theorists initially expected?

Time also comes into play when one considers the intergenerational transmission of attachment. To date, transmission has been assumed to be a single-generation process (e.g., a mother's attachment status shapes her child's attachment status via her parenting), with little consideration of the possible impact of grandparents, great-grandparents, and so forth. The evolutionary concept of intergenerational phenotypic inertia (Kuzawa, 2005), however, suggests that some forms of influence may endure across multiple generations, even when the most proximate generational experiences are at odds with the modal family trajectory. In particular, this model proposes that individuals should place greater diagnostic weight on conditions that have endured over multiple generations (e.g., repeated insecurity) rather than just the preceding one (e.g., one case of security), especially when the latter is inconsistent with the former. One might wonder whether an exclusive focus on the immediately preceding generation accounts in part for the intergenerational "transmission gap" that Van IJzendoorn (1995) identified.

This raises another set of issues. Although evolutionary forces should have shaped developmental trajectories, organisms also evolved to respond adaptively to rapid changes in local environments. The field of behavioral ecology, in fact, models such adaptive behaviors (see Gangestad & Simpson, 2007). In addition, the strategic pluralism model (Gangestad & Simpson, 2000) proposes that human females evolved to base mating decisions (including decisions about parenting qualities in mates) on two dimensions—the extent to which prospective mates display evidence of (1) viability (i.e., good health or other desirable mate-attracting attributes that could be passed

on genetically to offspring) and (2) investment potential (in both the romantic relationship and any resulting offspring). In pathogen-prevalent environments, women should place more weight on men's viability attributes, so the "good genes" of such mates might be passed on to their children. In environments that demand heavy investment in children or biparental care, women should place greater importance on men's investment potential to enhance the likelihood of offspring survival. Given their different life experiences, adults who have different attachment histories and styles may evaluate, calibrate, or apply each mate dimension somewhat differently. This returns us to the mate value of relationship partners. Avoidant women, for instance, may expect and require less paternal investment in light of their independence and self-reliance and, given their mistrust of others, they may want less. Anxious women, in contrast, may expect and demand greater investment given their chronic concerns about relationship loss and abandonment.

Epigenetics research may also advance our understanding of intergenerational attachment issues. Animal research has shown that maternal grooming of newborn female rat pups does not just calibrate pups' stress-response system when they are adults and raise their own offspring; through nongenetic mechanisms, such care also influences the development of the *grand-offspring* of the original grooming mother (Cameron et al., 2005). These findings are important because they partially explain the attachment-mothering intergenerational cycle, in that rearing experiences stimulate gene action, which launches a cascade of developmental processes and outcomes leading to different reproductive strategies in adulthood, which are then transmitted intergenerationally by nongenetic means. This evidence raises further intriguing questions about possible gene \times environment interactions; indeed, work by Caspi and colleagues (2002) supports differential susceptibility to parental influence by showing that the impact of rearing effects (e.g., child maltreatment) on the development of opportunistic, antisocial behavior varies depending on genotype. What remains unclear, however, is whether individuals who possess genetic "vulnerabilities" succumb to environmental risks, or whether early rearing experiences activate certain genes that then facilitate opportunistic, antisocial behavior.

Finally, like all too many developmental scientists who lack foundational knowledge about evolutionary theory, virtually all thinking and

writing to date about attachment (and even the development of reproductive strategies) has presumed that malleable children have their development regulated primarily by their rearing experiences. Yet as Trivers (1974) pointed out more than four decades ago, the fact that parents and children share on average only 50% of their genes means that their biological interests are not isomorphic, and they are therefore bound to experience conflicts of interest (see also Schlomer, Del Giudice, & Ellis, 2011). Del Giudice (2012) has noted that this may explain why children—even highly malleable ones—do not simply "take instructions" from their parents. What are the implications of this observation for understanding the development of attachment patterns specifically and for developmental plasticity more generally?

In conclusion, attachment theory is an evolutionary theory of human social behavior "from the cradle to the grave" (Bowlby, 1979, p. 129). Although the theory's initial ties to evolution focused on how the normative and individual-difference components of attachment should have promoted infant survival, recent work has revealed how attachment patterns across the lifespan—including adult romantic attachment styles—may have evolved to increase reproductive fitness. These theoretical advances are important for several reasons. Until recently, attachment theorists have not addressed *why* early developmental experiences should be systematically related to later life outcomes, *why* intergenerational transmission of attachment should exist, or *why* maternal sensitivity should shape attachment security in children. Traditionally, attachment theorists and researchers have focused on *how* these processes work. Recent applications of LHT *within* attachment theory have rectified this deficiency, directing attention to questions of both ultimate *and* proximate causation. These theoretical advances are also important because they suggest that adult attachment styles might *not* be inconsequential evolutionary "artifacts" of the attachment system in children. According to life history accounts, the attachment system in young children should have facilitated survival and development through the perilous years of early childhood, not just psychological health and well-being. In adulthood, the attachment system may further enhance inclusive fitness via the adoption of environmentally contingent, alternative reproductive strategies, not just satisfaction and happiness in close relationships.

In the future, attachment scholars need to anchor more of their thinking and research within a modern evolutionary framework. As Dobzhansky (1973) once exclaimed, “Nothing in biology makes sense except in the light of evolution” (p. 125). The same claim applies to much of psychology in general, and to much of developmental and social psychology in particular. We strongly advocate treading the intellectual path first paved by Darwin and extended by Bowlby and other modern evolutionary theorists. Various middle-level evolutionary theories—especially parent–offspring conflict theory, parental investment and sexual selection theory, and a life-history framework—have a tremendous amount to offer scholars interested in attachment phenomena across the lifespan. Significant future advances in attachment theory and research are likely to rest on the successful and complete integration of attachment theory into a modern evolutionary perspective.

Note

1. The term *strategy* refers to a set of coevolved anatomical, physiological, psychological, and/or behavioral traits designed by natural selection to increase inclusive fitness. It does *not* imply foresight, conscious awareness, or premeditation. The term *optimal* does *not* imply that natural selection produces a single, perfect phenotype. *Optimal strategies* are sets of coevolved traits that tend to increase inclusive fitness in specific environments given various tradeoffs.

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