CHAPTER 6

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.


As this quotation suggests, Charles Darwin may have been the first attachment theorist. Although he focused on “society” (instead of significant persons in an individual’s life) and “comrades” (instead of attachment figures), Darwin was perhaps the first scientist to appreciate the deep degree to which human social nature is a product of selection pressures. John Bowlby, who admired Darwin’s theoretical vision and was one of his biographers (see Bowlby, 1991), spent most of his brilliant career treading the intellectual path that Darwin began 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—attachment theory. Among the reasons why attachment theory is so unique, generative, and prominent today are its deep intellectual ties to fundamental principles of evolution.

Indeed, attachment theory is one of a handful of major middle-level evolutionary theories. 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 vehemently, 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, particularly in species born in a developmentally immature and highly dependent state. 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 motor activity declines and they fall silent. From an evolutionary standpoint, Bowlby realized that dependency is a good “second” strategy to promote survival. Excessive movement may 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 is to avoid actions that may increase the risks of self-inflicted harm or predation.

Bowlby observed that after a period of despair, infants who are not reunited with their caregivers enter a third and final stage—detachment. During this phase, an 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 partially if not fully relinquished before new bonds can be formed. From the standpoint of evolution, detachment allows infants to cut off old ties and begin the process of forming new ones with caregivers who may be willing to provide the resources necessary for survival.

Bowlby believed that the cognitive, emotional, and behavioral reactions characterizing each stage reveal the operation of an innate attachment system. The 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 daunting adaptive problems our ancestors faced: how to increase the probability of survival through the most perilous years of social and physical development. Guided by Darwin, Bowlby believed that the attachment system was genetically “wired” into many species through intense 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 corrected during the development of attachment theory (see Belsky, 1999; Bowlby, 1969/1982; Simpson, 1999). One shortcoming was Bowlby’s initial focus on the differential survival of species rather than of individuals. Another shortcoming was his nearly exclusive focus on the survival function of attachment rather than its implications for differential reproduction. To enhance reproductive fitness, individuals must not only survive to reproductive age; once there, they must successfully mate and raise children, who in turn must mate and raise their own children, and so on. Fortunately, as we shall see, contemporary attachment theorists have shifted attention to how attachment phenomena and processes in childhood may be systematically linked to the enactment of different reproductive strategies in adulthood (Belsky, 2007; Belsky, Steinberg, & Draper, 1991; Chisholm, 1996, 1999). Nevertheless, because individuals cannot reproduce without first surviving to reproductive age, Bowlby was wise to build the foundation of attachment theory on this vital prerequisite to ultimate reproductive fitness.

Early attachment theorists also harbored the erroneous view that most rearing environments in the “environment of evolutionary adaptedness” (EEA) were benign, resulting in the secure attachment pattern being “species-typical” (see Ainsworth, 1979; Main, 1981). The EEA, however, was probably not nearly as uniform, resource-rich, or benign as many early attachment theorists envisioned (Edgerton, 1992; Foley, 1992), meaning 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) may actually reflect evolved, unpremeditated tactics designed to improve reproductive fitness in response to the specific environments in which individuals grow and develop. “Reproductive fitness” reflects the extent to which an individual’s genes are present in his or her descendants. The concept of “inclusive fitness” (see 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.

Perhaps the biggest impediment to Bowlby’s understanding of evolution, however, was the nascent 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 important “middle-level” theories of evolution—theories addressing the major adaptive problems that humans probably confronted at different life stages during evolutionary history—were introduced in the early to mid-1970s. As a result, Bowlby was not privy to much of what is now known as the “modern” evolutionary perspective when he began erecting the tenets of attachment theory. Until recently, few of the modern middle-level evolutionary theories have been 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. As will become apparent, the modern evolutionary perspective includes an array of theories, principles, and assumptions, all of which share a central premise: that much of the human mind and human social
behavior reflect adaptations to the major obstacles to inclusive fitness that humans repeatedly faced throughout evolutionary history.

The chapter is divided into seven sections. The first section briefly reviews theoretical developments that have transformed Darwin's (1859, 1871/1981) 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 most likely inhabited in the past 100,000 years. Highlighting anthropological evidence from hunter-gatherer tribes, we identify the most stable features of the social EEA's that humans probably inhabited.

The third section focuses on 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 and unfold across the lifespan. Different patterns or styles of attachment are construed as adaptive, ecologically contingent behavioral strategies that could have facilitated reproduction in adulthood, given the probable environments that individuals would inhabit as adults.

The fourth section 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 children'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 may affect the trajectory of social and personality development, culminating in divergent reproductive strategies in adulthood. In the final two sections, we highlight some important 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, especially in view of recent theoretical advances that have shaped the modern evolutionary perspective. Darwin's thinking was constrained by several factors. First, his theory predated our understanding of genes and patterns of inheritance. Mendel's pioneering research on heritable traits in plants, though initially published in 1866, was neither understood nor appreciated until well after the turn of the 20th century. 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 and provided compelling empirical evidence for the concept of inclusive fitness (i.e., the notion that differential gene replication really 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, Darwin did not fully appreciate the extent to which specific adaptations are associated with both benefits and costs. Similar to many theorists of his time, he focused more on the benefits bestowed by certain adaptations and did not fully consider potential costs (see Cronin, 1991). Darwin's brilliance allowed him to sketch the ways in which natural selection might operate, without the benefits of all this knowledge.

The Rise of Modern Evolutionary Theories

Few theoretical advances occurred in the evolutionary sciences for almost a century after Darwin published his second landmark book, The Descent of Man, in 1871. This state of affairs changed in the mid-1960s. With the development of inclusive fitness theory, Hamilton (1964) introduced the notion of 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, in the evolutionary struggle for reproductive fitness, why do 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 should depend 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 may be
situations in which it would pay to sacrifice one's own reproductive output, including one's life, in order 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-quarter of their genes with their grandchildren; aunts and uncles share one-quarter 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, although it would make sense to sacrifice one's own life to save at least two biological children (each of whom shares 50% of a 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 critical barrier to inclusive fitness—how to survive the many perils and dangers of infancy.

Several important theoretical advances followed in the early 1970s, many of which were spearheaded by Robert Trivers. In 1971, he introduced the theory of reciprocal altruism, which explains why organisms who have inherently "selfish" genes should at times behave in a cooperative manner with non-kin. Trivers outlined some of the specific conditions under which selective reciprocal altruism could enhance an individual's inclusive fitness. Axelrod (1984) then demonstrated how a quid pro quo strategy of helping others (i.e., a tit-for-tat strategy) could evolve and become stable amid alternate 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 (1972) argued that in species where 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.

In 1974, Trivers introduced the theory of parent–offspring conflict. This theory 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 the theory of parent–offspring conflict has several fascinating implications for how patterns of attachment between children and their caregivers can be understood, we discuss it in greater detail below.

In recent years, life history theory (LHT; Charnov, 1993; Clutton-Brock, 1991; Stearns, 1976, 1992; Williams, 1966) has become a prominent, unifying perspective within the evolutionary sciences. In order to leave descendants, individuals must solve multiple problems tied to survival, growth, development, and reproduction across the lifespan. Depending on life circumstances, the time, effort, and energy that an individual has can be allotted to somatic effort (i.e., investing in growth and development of one's body to facilitate survival en route to later reproduction) and reproductive effort (i.e., funneling effort toward progeny). Reproductive effort, in turn, 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). LHT addresses how individuals should best allocate somatic versus reproductive effort, given their past, current, and anticipated (future) life circumstances.

**Attachment Theory in the Hierarchy of Evolutionary Theories**

Inclusive fitness theory, which encompasses Darwin's concept of fitness due to one's own reproduction (i.e., direct descendants—children) as
well as 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 nearly all middle-level evolutionary theories flow. The middle-level theories, each of which addresses special adaptive problems that humans faced during evolutionary history, reside one level below inclusive fitness theory, being more specific and less general. As discussed above, some of the major middle-level theories are reciprocal altruism theory (Trivers, 1971), sexual selection and parental investment theory (Trivers, 1972), parent–offspring conflict theory (Trivers, 1974), and attachment theory (Bowlby, 1969/1982). Because it addresses how individuals should allocate their finite resources across the entire lifespan, LHT (Charnov, 1993; Stearns, 1992) intersects with and interconnects many of the other middle-level theories. Each middle-level theory contains 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 extent to which prospective mates (1) are likely to be good investors in and providers for future offspring, and (2) possess desirable attributes (e.g., physical attractiveness or other mate-attracting features) that can 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 infants feel ill, fatigued, afraid, or upset (Bowlby, 1969/1982). The individual-difference component offers predictions about the ontogenetic 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 was formulated to address a specific adaptive problem, many of them have overlapping implications for social behavior. The theory of kin selection, for example, also stipulates when conflict ought to arise between parents and their children; the theory of parent–offspring conflict specifies when reciprocal altruism should emerge between different sets of parents; and the theory of reciprocal altruism addresses when men and women may strive to attain status and ascend social hierarchies in local groups (see Simpson, 1999). Moreover, in some cases, middle-level theories generate different hypotheses and predictions about a given outcome. This highlights a critical point: For some phenomena, there is no single evolutionary prediction, particularly if competing middle-level theories are involved (see Buss, 1995).

### STABLE FEATURES OF THE SOCIAL EEA

To gain a clearer understanding of 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 probably inhabited in evolutionary history. Although attachment theorists have speculated some about what the EEA might have been like (especially the physical EEA; see Bowlby, 1969/1982), less consideration has been given to the social EEA (for an exception, see Brewer & Caporael, 1990, 2006). Unfortunately, we do not know many concrete details about the environments in which our ancestors lived. What we do know is that, given their diverse migration patterns, humans inhabited a wide array of geographical and climatic environments, ranging from arid and barren deserts to lush tropical jungles. Thus there was no single EEA, particularly no monolithic physical environment. The social environments in which most humans evolved, however, may have had some reasonably consistent and stable features (see Simpson, 1999).

During much of human evolutionary history, for example, people were hunters and gatherers (Cronk, 1999; Kelly, 1995). Anthropological observations of contemporary hunter-gatherer tribes, such as the !Kung San of Africa, the Inuit of the Arctic, the Ache of Paraguay, and the Aborigines of Australia, provide perhaps the best views of what ancient tribal life might have been like. For thousands of generations, our ancestors lived in small, cooperative groups (Brewer & Caporael, 1990; Eibl-Eibesfeldt, 1989). Most people within a tribe were biologically related to one another, and strangers were encountered rather infrequently, probably during intertribal trading or war (Wright, 1994). Though people occasionally migrated in and out of their natal groups, most remained in the same tribe their entire lives.
Most men and women formed long-term pair bonds (Cronk, 1999), but serial monogamy was probably the norm (Fisher, 1992). Children were typically born approximately 4 years apart and were raised with considerable help from extended family and perhaps non-kin (Wright, 1994); few children were raised exclusively by their biological parents. In fact, humans were probably “cooperative breeders” who shared childrearing with their kin (Hrdy, 1999, 2005). In all likelihood, younger children spent considerable time being socialized by older children (Eibl-Eibesfeldt, 1989). 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). Whereas some of these inferences are more speculative than others, the human mind probably evolved to deal with problems arising in social environments that had these features. Indeed, participation in the daily functioning of small, cooperative groups may have been the predominant survival strategy of early humans (Brewer & Caporael, 1990). These likely features of the social EEA must be considered when attachment theory is conceptualized within an evolutionary framework.

NORMATIVE AND INDIVIDUAL-DIFFERENCE COMPONENTS OF ATTACHMENT

As mentioned earlier, attachment theory has two primary components: (1) a normative component, which seeks to explain 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, which attempts to explain deviations from modal or normative patterns and stages (e.g., “How and why do different patterns of attachment exist?”). The attempt to explain both species-typical patterns of behavior and predictable individual differences is a hallmark of most major middle-level evolutionary theories (Simpson, 1999). Bowlby and Ainsworth were, in fact, among the first middle-level evolutionary theorists to recognize the need to explain not only normative behavior, but systematic individual differences as well.

Normative Features of Attachment

There are several normative features of attachment, three of which have especially important ties to evolutionary principles: the apparent “synchronization” of infant–parent responses/behaviors in the opening months of life; young children’s need to maintain contact with and seek proximity to their caregivers; and basic stages through which attachment propensities develop.

Synchronized Capabilities

Compared to 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 (see Simpson, 1999). In addition, several postpartum reactions of mothers seem to operate in synchrony with those of their newborns, facilitating the early formation of infant–caregiver bonds. Systems that operate in a synchronous, lock-and-key fashion between codependent individuals are often telltale signs of evolved adaptations (Andrews, Gangestad, & Matthews, 2002).

Immediately after delivery, for example, mothers experience a rush of hormones that make them feel euphoric and receptive to emotional bonding, despite the fact that they are exhausted from giving birth (Eibl-Eibesfeldt, 1989). Without instruction, mothers in all cultures place themselves about 30 centimeters from their young infants, which happens to be an optimal distance for young infants to see faces clearly (Eibl-Eibesfeldt, 1989). Mothers also work hard to establish eye contact with their infants (Klaus & Kennell, 1976), and when infants reciprocate eye contact, mothers become livelier, speak with greater voice inflections, and approach their infants more closely (Grossmann, 1978, cited in Eibl-Eibesfeldt, 1989). Eye contact and smiling by infants are extremely rewarding to new mothers, who interpret such cues as signs of genuine affection (Eibl-Eibesfeldt, 1989). When interacting with their infants, mothers typically exaggerate their facial expressions, change them more slowly, and maintain visual contact for longer periods of time (Eibl-Eibesfeldt, 1989), all of which are ideally suited to an infant’s developing visual system. When talking to their infants, mothers intentionally slow their speech, accentuate certain syllables, and talk one octave above normal speech (Anderson & Jaffe, 1972; Grieser & Kuhl, 1988). This pattern of speech, termed “motherese,” is preferred by most young infants (Fernald, 1985) and is well suited to infants’ developing auditory capacities. It is simply plausible that such well-coordinated and interconnected behaviors and proclivities did not coevolve. The evolutionary hypothesis is that by tying mother to baby and baby to mother, these
coordinated responses, skills, and inclinations promoted the survival and probably the reproductive fitness of mothers and their children.

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 that establish or maintain proximity to their caregivers (Belsky & Cassidy, 1994). Signal behaviors (e.g., vocalizing, smiling) tend to draw caregivers toward children, usually for positive interactions. Aversive behaviors (e.g., crying, screaming) bring caregivers to children, typically to terminate the aversive reactions. Active behaviors (e.g., approaching, following) move children toward caregivers. Though different phenotypically, these behaviors all serve the same biological function: to keep vulnerable infants in close physical proximity to their caregivers, thereby increasing their chances of survival. Given that death prior to reproduction was the first major threat to inclusive fitness, Bowlby reasoned that directional selection shaped the attachment system in humans, setting the foundation of our social nature.

Phases of Development

According to Bowlby (1969/1982, see Marvin & Britner, Chapter 12, this volume), attachment propensities develop through four phases in humans. In the first phase, which takes place between birth and 2–3 months, infants respond to a variety of social stimuli and people, not exhibiting strong preferences for one attachment figure. Although Bowlby may have overestimated how open very young infants are to contact comfort from multiple caregivers (see above), he was correct in believing that infants are malleable in terms of whom they can bond with in the opening months of life. During the second phase, which runs from 2–3 months to about 7 months, infants display greater discrimination in social responsiveness. They begin, for instance, to distinguish caregivers and family members from strangers, to selectively prefer certain persons, and to direct their attachment behaviors toward specific attachment figures.

In the third phase, which extends from 7 months to roughly 3 years, children learn to play a more active role in seeking proximity and initiating social contact. During this phase, they start to develop “internal working models” (i.e., beliefs, expectancies, and attitudes about relationships based on experiences with attachment figures) of the self and significant others (Bowlby, 1973). This is also the phase during which the three primary functions of attachment are first seen in the child’s behavior: proximity maintenance (staying near to, and resisting 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. The fourth phase, which begins at about age 3, marks the beginning of behaviors that signal the development of a “goal-directed partnership” with attachment figures. That is, given the further development of language skills and theory-of-mind capabilities, children begin to see the world from the perspective of their interaction partners. This allows them to incorporate the goals, plans, and desires of their interaction partners into their decision making, resulting in the negotiation of joint plans and activities.

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; Streuf & Waters, 1977). Early in adolescence, overt manifestations of attachment bonds with parents start to subside (Hinde, 1976). The three functions of attachment—proximity maintenance, safe haven, and secure base—are slowly transferred from parents to peers and romantic partners as adolescents enter adulthood (see Furman & Simon, 1999; Hazan & Shaver, 1994).

In summary, each of these normative capabilities and proclivities was probably shaped by selection pressures. Infants (and mothers) who forged stronger emotional bonds had, on average, higher reproductive fitness. Young children who were motivated to maintain closer contact to their parents (and parents who encouraged such tendencies) achieved greater fitness, as did individuals who successfully moved through each attachment stage and were able to transfer critical attachment functions from their parents to adult romantic partners.

Individual Differences in Attachment

Although infants are biologically predisposed to form attachment bonds with their caregivers, the
type of bonds they form ought to depend on the conditions in which they are raised, just as Bowlby (1969/1982) and Ainsworth (1979) argued. Perceptions of environmental conditions, in turn, are likely to be filtered through evolved psychological mechanisms. Psychological mechanisms are typically activated by specific environmental cues, resulting in "optimal" ecologically contingent strategies that evolved to solve specific adaptive problems posed by different kinds of environments (see Buss, 1995; Tooby & Cosmides, 1992). The term "strategy" refers to a set of coevolved anatomical, physiological, psychological, and/or behavioral traits designed by natural selection to increase inclusive fitness. Use of this term does not imply foresight, conscious awareness, or premeditation. In addition, the term "optimal" does not imply that natural selection is geared to produce a single, perfect phenotype. Optimal strategies are sets of coevolved traits that are best suited to increasing inclusive fitness in specific environments, given various tradeoffs.

Infants, of course, do not have the cognitive ability to appraise the quality of local environmental conditions (e.g., whether the environment is safe, plentiful, and rich in resources vs. threatening, harsh, and impoverished). However, they do have the ability to determine whether their 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; Belsky et al., 1991; Chisholm, 1996). 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). 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, usually resuming other activities (e.g., exploration, play) 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, often intermingling clingingness with outbursts of anger (what Bowlby [1973] termed the "anger of hope").

Each attachment pattern reflects a different "strategy" that could have solved adaptive problems presented by different kinds of rearing environments (see 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). In particular, they are attuned to signs that their infants are distressed (Del Carmen, Pedersen, Huffman, & Bryan, 1993; provide moderate and appropriate levels of stimulation (Belsky, Rovine, & Taylor, 1984; Feldstein, Crown, Beebe, & Jaffe, 1995); engage in synchronous interactions with their infants (Isabella & Belsky, 1990; Isabella, Belsky, & von Eye, 1989; Leyendecker, Lamb, & Scholmerich, in press); and behave in a warm, involved, and contingently responsive manner (Braungartner, Rieker, Garwood, Powers, & Wang, 2001; National Institute of Child Health and Human Development [NICHD] Early Child Care Network, 1997). Partly because their caregivers are sensitive and responsive, secure children need not worry about the availability and responsiveness of their caregivers, which permits them to concentrate on other life tasks.

Anxious-ambivalent children, in contrast, have caregivers who behave inconsistently toward them (Ainsworth et al., 1978), sometimes because of poor or deficient parenting skills. Mothers of such infants tend to respond erratically to their infants' needs and signals, sometimes appearing to be underinvolved parents (Belsky et al., 1984; Isabella et al., 1989; Lewis & Feiring, 1989; Scholmerich, Fracasso, Lamb, & Broberg, 1995; Smith & Pedersen, 1988; Vondra, Shaw, & Kevinsides, 1995). 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 ambivalent children might reflect an ecologically contingent strategy designed to obtain, retain, or improve greater parental attention and care (Cassidy & Berlin, 1994; Main & Solomon, 1986). More specifically, the constellation of behaviors characteristic of ambivalent children—including hyper-
vigilance and rumination about potential relationship loss (Cassidy & Berlin, 1994)—could have evolved to counteract deficiencies in caregiving by young, naive, overburdened, or underinvolved parents. For children who had such parents, this behavioral strategy would have increased proximity to caregivers, solicited better care, and improved their chances of survival. In view of cross-cultural evidence indicating that insecure infants in Israel are disproportionately likely to develop anxious-ambivalent attachments (van IJzendoorn & Sagi-Schwartz, Chapter 37, this volume), this pattern might also have been an evolved strategy for inducing helpless dependency in order to keep children excessively close in a world filled not only with strangers, but with people who had actually harmed biological relatives in the past.

Anxious-avoidant children usually have caregivers who are cold and rejecting (Ainsworth et al., 1978). Indeed, mothers of avoidant children are less responsive to their infants’ distress (Crockenberg, 1981), use overly stimulating styles of interaction (Belsky et al., 1984; Scholmerich et al., 1995; Vondra et al., 1995), and dislike close body contact (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 anxious avoidance, however, may be more complex and multifaceted than the origins of anxious ambivalence. Bowlby (1980) conjectured that avoidance allows infants to disregard cues that may 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 further evolutionary explanations for avoidance in childhood have been developed. Main (1981) suggests that the distant, self-reliant behavior characteristic of avoidant infants permits them to maintain reasonably close proximity to belligerent or overwhelmed caregivers without driving them away. Avoidance, in other words, might have evolved to overcome deficiencies in caregiving provided by highly distressed, hostile, or unmotivated parents. During evolutionary history, this behavioral strategy would have increased survival among infants who, if they placed too many demands on their parents, might have been abandoned. Alternately, earlier reproduction might have facilitated inclusive fitness in some circumstances, especially in harsh environments with few resources (Trivers, 1985). If maternal rejection served as a proximal cue of the severity of future environments, avoidant tendencies might have allowed children not only to move away from their parents earlier, but to become more opportunistic and advantage-taking, thereby facilitating survival and early reproduction in such anxious environments (Belsky, 1997; Belsky et al., 1991).

Given the complex neural foundations of the attachment system (see Simpson, Beckes, & Weisberg, 2007), the basic functions of the attachment system ought to be fairly consistent across the lifespan. As children enter adolescence, however, cumulative experiences in relationships should be assimilated into internal working models, which are continually 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 (Bartholomew & Horowitz, 1991; Collins & Read, 1994). Unlike the attachment system in childhood, adulthood the system becomes integrated with the mating and caregiving systems (Kirkpatrick, 1998; Shaver, Hazan, & Bradshaw, 1988; Zeifman & Hazan, 1997). The infusion of these other systems makes 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, parents who share 50% of their genes with parents and full siblings) should desire greater investment from their parents than their parents have been selected to provide. As a result, parents and offspring ought to have slightly divergent reproductive interests, resulting in bouts of conflict that climax during the final stages of weaning.

Parent–Offspring Conflict Theory and Parental Investment

According to Trivers (1972), parental investment includes 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 offspring (including current or future children). The level of investment is a function of the costs and benefits associated with a given parental act or behavior. “Costs” are defined as units of foregone reproductive success by any
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 such activities as feeding, protecting, sheltering, and teaching. The amount of investment that children seek and parents offer should depend on how both parties view the costs and benefits of different forms of parental investment. Hamilton (1964), for example, has shown that altruistic behaviors (i.e., acts that lower an individual’s future reproductive success while raising the recipient’s success) could have evolved if beneficiaries were biological relatives who carried the same altruistic genes. When $1 < \frac{b - c}{c}$ (where $\tau$ = the degree of relatedness, $b = \text{benefits of an altruistic act}$, and $c = \text{costs of the act}$), altruism would have increased inclusive fitness and been selected.

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. However, as infants grow, consume more resources, and become more self-sufficient, the reproductive interests of parents and offspring diverge. From a parent’s perspective, the costs of investment continue to rise over time, while the benefits an infant derives from additional investment reach an asymptote. During this phase, directing investment to new offspring may 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 many cultures.

Because children share only half of their genes with their parents and full siblings, two of an infant’s siblings must survive and successfully reproduce to fully propagate the infant’s genes to future generations. Accordingly, 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. A child and parent, 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 will be reduced if he or she continues to demand additional investment. Conflict should then subside as the child accepts the diversion of parental investment to other siblings.

Trivers (1974) hypothesized that the intensity and duration of parent-offspring conflict should also depend on factors that affect the cost-benefit ratio over time. Several novel predictions flow from the theory. For instance, conflict should be greater when there are stepsiblings in families. Because stepsiblings share only 25% of their genes, four stepsiblings must survive and reproduce to fully propagate a child’s genes. Within “pure” stepfamilies, therefore, offspring should demand approximately four times as much investment as their parents are willing to grant, resulting in unusually long and intense periods of parent-offspring conflict. Conflict should also be more pronounced in families with very young mothers. Because younger mothers have more reproductive years ahead of them (and therefore more and possibly better reproductive opportunities in the future) than older mothers do, younger mothers should be less tolerant of high-cost infants.

Attachment theory does not fully recognize and account for the slightly different reproductive interests of infants and their caregivers (see Main, 1990). Indeed, many attachment theorists assume that the evolutionary interests of parents and their children are equivalent, and that (harming 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); 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 discriminative parental solicitude (i.e., preferential investment in certain children; Daly & Wilson, 1981). In some instances, attachment insecurity may arise from conditions that lower parental investment. Lower investment should be revealed by inadequate or poor caregiving behaviors, including parental inattentiveness, neglect, rejection, abuse, and even infanticide in extreme cases.1

Cross-cultural research indicates that parental investment is in fact lower when a family contains
at least one stepparent; 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 (see Daly & Wilson, 1984, 1988; Dickemann, 1973; Hrdy, 1999; Minturn & Stashak, 1982, for reviews). The incidence of parental neglect, abuse, and occasional infanticide increases sharply when certain conditions are present. For example, when adjustments are made for the prevalence of stepfamilies, the probability of child abuse is up to 100 times greater in households containing at least one stepparent than in households that have two biological parents (Daly & Wilson, 1985). Stepparents, especially stepfathers, are many times more likely to kill their biologically unrelated stepchildren than biological parents are to kill their children (Daly & Wilson, 1988). If biological parents maltreat their children, they typically engage in neglect rather than more active abuse, and usually for reasons associated with poverty (Daly & Wilson, 1981). Moreover, even when financial resources and marital status are statistically controlled for, younger mothers are more likely to kill their infants than are older mothers (Daly & Wilson, 1988), and older mothers are much less likely to abuse or harm their infants (Daly & Wilson, 1985).

From an evolutionary perspective, each of the precipitating conditions listed above should have incrementally deleterious effects on the quality and/or quantity of parent–infant interactions, setting the stage for insecure attachment patterns. For children who have congenital disabilities (e.g., blindness, mental retardation, severe emotional disturbances), or for mothers who feel overburdened (due to youth, depression, lack of paternal investment, or inadequate social support), neonatal emotional bonding may be disrupted by limited mother–infant postpartum contact or the inability of mothers and their infants to communicate in ways that facilitate early bonding (Daly & Wilson, 1981). Some evidence suggests that mothers deprived of postpartum interaction sometimes report feeling emotionally detached from their infants (Kennell, Trause, & Klaus, 1975). Infants separated from their mothers during the first few days of life may be slightly more likely to be abused as toddlers (Klaus & Kennell, 1976; Lynch, 1975; O'Conner, Vietze, Hopkins, & Altemeier, 1977) and both disabled children and overburdened mothers are more likely to have experienced early separations (Irvin, Kennell, & Klaus, 1976; Sugarman, 1977). If these precipitating conditions persist over time, this may reinforce poor, insensitive, or noncontingent caregiving.

**Parental Investment and Attachment**

Relatively little is known about whether the conditions that should reduce parental investment cause insecure attachment in children. Certain contextual factors, however, predict the development of insecure patterns (see Belsky & Feinon, Chapter 13, this volume). For example, parents who have better psychological health and well-being typically provide their offspring with higher-quality care (Belsky, 1984; Gelfand & Teti, 1990), and their children tend to be securely attached (Belsky & Isabella, 1988; Benn, 1986; NICHD Early Child Care Network, 1997; O'Connor, 1997). And clinically depressed mothers, who tend to display intrusive/hostile or detached/unresponsive styles of caregiving (Belsky & Jaffe, 2006), are more likely to have insecurely attached infants (for a meta-analysis, see Atkinson et al., 2000).

In addition, spouses involved in happier and more supportive marriages when their children are infants and toddlers exhibit better and more sensitive parenting skills (for reviews, see Belsky & Jaffe, 2006; Krishnakumar & Bucher, 2000), and as a result have securely attached infants (Goldberg & Easterbrooks, 1984; Howes & Markman, 1989; Teti, Gelfand, Messinger, & Isabella, 1995). Spouses who display the lowest levels of parental support are more likely to have infants with the most severe form of insecurity—the disorganized/disoriented (D) attachment pattern (Spieker, 1988; Spieker & Booth, 1988). Isabella (1994) has found that the relation between marital quality and infant attachment is mediated by maternal role satisfaction and maternal sensitivity to the child's needs.

External social support also has a positive impact on both parenting behavior and attachment security in infants and young children. Mothers who perceive more support from the community interact with their infants more positively (for a meta-analysis, see Andersen & Telleen, 1992), whereas those who perceive less support provide less sensitive care (Smith, Landry, & Swank, 2000). Poor mothers given material resources are more likely to hold, touch, kiss, and vocalize with their young infants (Feiring, Fox, Jaskir, & Lewis, 1987). Indeed, in samples of high-risk infants, the level of social support that mothers receive correlates positively with the long-term attachment security of their children (Cronin, Greenberg, & Slough, 1986), which is mediated by the quality of
mothers' daily care (Crittenden, 1985). Although some studies have found no connection between social support and attachment security (e.g., Zeannah et al., 1993), several experimental studies have confirmed this link (e.g., Jacobson & Frye, 1991; Lieberman, Weston, & Pawl, 1991; Lyons-Ruth, Connell, & Grunebaum, 1990).

In summary, parent–offspring conflict theory offers novel insights into the conditions that should, from an evolutionary perspective, reduce parental investment. Attachment theorists have not taken full advantage of these and other insights (see Belsky, 1999; Simpson, 1999). Although the level of caregiver sensitivity appears to be one of the proximal causes of secure versus insecure attachment in infants and young children (van Ijzendoorn, 1995b), attachment theorists need to consider the full range of contextual factors that, from the vantage point of ultimate causation, should govern caregiver sensitivity.

**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 related to mating and reproduction). Even though some early attachment theorists (e.g., Main, 1981) conjectured that different attachment patterns observed in children might reflect different evolution-based strategies for promoting survival under certain rearing conditions, childhood attachment patterns were not systematically 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 ideas from LHT (Charnov, 1993; Stearns, 1992). LHT (see Kaplan & Gangestad, 2005, for a recent review) addresses how and why individuals allocate time, energy, and resources to different traits, behaviors, and life tasks when they make tradeoff decisions that could influence their reproductive fitness. 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 will affect the timing of their mortality (i.e., the age at which they deteriorate and 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 may 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 enhances it once individuals mature sexually (Sterns, 1992).

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.

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. How each tradeoff is resolved should depend on several factors, including the demands of the local environment (e.g., how taxing it is, the amount of pathogens it contains, whether biparental care is required); the skills, abilities, and resources available to an individual at that time; the skills, abilities, and resources possessed by others (e.g., kin, potential mates, competitors); and so on.

**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 major evolution-based 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 inhabit during their lifetime. The model focuses primarily on offspring quantity versus quality tradeoffs. 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 fail to display these attributes. Conversely, offspring raised in environments with abundant resources could increase their fitness by adopting a more cooperative and communal orientation toward others in adulthood.

The Belsky and colleagues (1991) model includes five stages. It proposes that (1) early contextual factors in the family of origin (e.g., level of stress, spousal harmony, financial resources) affect (2) early child-rearing 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), which in turn influences (4) somatic development (how quickly sexual maturation is reached) and eventually (5) the adoption of specific reproductive strategies. Although Belsky and colleagues suggested that these stages are linked sequentially, they also suggested that earlier stages may statistically interact to predict later outcomes (see Belsky, 2007). Early contextual factors in the family of origin, for example, may interact with early child-rearing experiences to forecast the rate of somatic development.

Belsky and colleagues (1991) hypothesized that two developmental trajectories culminate in two distinct reproductive strategies in adulthood (although they also entertained the possibility that these may be opposite ends of a single continuum rather than alternate types). One strategy entails a short-term, opportunistic orientation toward close relationships (especially those pertaining 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 toward increasing the quantity of offspring. The second strategy entails a long-term, investing orientation toward mating relationships, in which sexual intercourse occurs later in life, romantic pair bonds are enduring, and parental investment is greater. This orientation focuses on maximizing offspring quality. A critical prediction derived from the model—one that distinguishes it from all other nonevolutionary theories of psychological and behavioral development—is that early rearing experiences should influence the timing of puberty. In particular, puberty should occur earlier for individuals who develop along the “quantity trajectory” than for those who develop along the “quality trajectory.” According to classical philosophy of science, a theory that explains what competing theories can explain, but also makes original predictions that other theories do not make, should supplant competing theories if its novel predictions prove accurate (see Ketelaar & Ellis, 2000).

A growing body of evidence supports the Belsky et al. model (for recent reviews, see Belsky, 2007; Ellis, 2004). For example, in accord with nonevolutionary perspectives, greater socioeconomic stress in families is related to more insensitive, harsh, rejecting, inconsistent, and/or unpredictable parenting practices. Economic hardship (Burgess & Draper, 1989; 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 seem to facilitate warmer and more sensitive child-rearing practices (Belsky, 2007; 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, in line with predictions from many theories, including classical attachment theory. During the first year of life, insensitive and unresponsive caregiving predicts the development of insecure attachments (see De Wolff & van IJzendoorn, 1997), which in turn predict assortative 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 display more severe behavior problems, especially aggression and disobedience (Erickson, Sroufe, & Egeland, 1985; Lewis, Feiring, McGuffog, & Jaskir, 1984). According to Belsky and colleagues (1991), these behaviors are governed by insecure working models, which "prepare" the child for negative, noncommunal relationships later in life. (For more recent evidence supporting the model, see Amato, 2001; Belsky & Fearon, 2002 and Chapter 13, this volume; Buehler & Gerard, 2002; Parke et al., 2004; Seccombe, 2000.)

As already noted, the most novel part of the model is the factors that predict the rate of somatic development. Belsky and colleagues (1991) claimed that children exposed to higher levels of socioemotional stress develop insecure attachments, exhibit behavior disorders, and should reach puberty—and therefore reproductive capacity—earlier than children without these attributes. According to LHT logic (Chisholm, 1993, 1999; Promislow & Harvey, 1990), environments in which resources are scarce and relationship ties are tenuous should cause more energy and effort to be allocated to rapid physical development, early mating, and short-term romantic pair bonds. Delayed maturation and reproduction in such arduous environments may cost individuals dearly, especially if they die before reproducing. On the other hand, environments in which resources are plentiful and relationship ties are reciprocal and enduring should result in efforts being channeled to additional 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.

Three strands of evidence support this novel feature of the Belsky and colleagues (1991) model. First, greater parent–child warmth, cohesion, and positivity predict delayed pubertal development in both prospective longitudinal studies (Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999; Oraber, Brooks-Gunn, & Warren, 1995; Steinberg, 1988) and retrospective or concurrent ones (Kim & Smith, 1998a; Kim, Smith, & Palermiti, 1997; Miller & Pasta, 2000; Romans, Martin, Gendall, & Herbison, 2003; Rowe, 2000). Second, greater parent–child conflict and coercion predict earlier pubertal timing in both prospective longitudinal studies (Moffitt, Caspi, Belsky, & Silva, 1992) and retrospective or concurrent ones (Jorm, Christensen, Rodgers, Jacomb, & Eastell, 2004; Kim & Smith, 1998a, 1998b; Kim et al., 1997; Mezzich et al., 1997; Wierson, Long, & Forehand, 1993).

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 those employing less rigorous research designs (Kim et al., 1997; Romans et al., 2003).

Virtually all of these findings are based on studies of girls, because of the difficulties associated with measuring pubertal development in boys. In the few studies that have examined boys, parallel pubertal timing effects have not been found (Ellis, 2004). Moreover, some studies have not found certain hypothesized links for girls. Ellis and colleagues (1999), Miller and Pasta (2000), and Steinberg (1988), for instance, did not find associations between the amount of family conflict/coercion and pubertal timing in girls. Nevertheless, in an outstanding comprehensive review of this literature, Ellis (2004, pp. 935–936) concluded that "empirical research has provided reasonable, though incomplete" support for the Belsky and colleagues model.

Evidence relevant to the final stages of the Belsky and colleagues (1991) model (i.e., the mating strategies that individuals adopt in adulthood) comes from two sources: (1) research tying 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 their romantic partners are less likely to have promiscuous sexual attitudes or to engage in sex with other partners (Brennan & Shaver, 1995; Simpson & Gangestad, 1991). Indeed, more securely attached adults claim that they would ideally desire only one sexual partner (mate) during the next 30 years (Miller & Fishkin, 1997), and more secure women tend to have first sexual intercourse at a later age than do insecure women (Bogaert & Sadava, 2002).

Satisfaction is also higher in the romantic relationships of more securely attached adults (J. Feeney, Chapter 21, this volume; Rholes, Simpson, Campbell, & Orich, 2001; Simpson, 1990), and observational research confirms that more secure adults display less negative affect and more constructive conflict resolution tactics when interacting with their romantic partners (J. Feeney,
Chapter 21, this volume; Simpson, Rholes, & Phillips, 1996). Greater attachment security is also related to better communication in romantic relationships, including greater self-disclosure and responsivity to self-disclosures by partners (Kobak & Hazan, 1991; Mikulincer & Nachson, 1991). In addition, more secure adults are less likely to divorce or separate from their partners (Kirkpatrick & Hazan, 1994; see B. Feeney & Monin, Chapter 39, this volume); they have longer-lasting romantic relationships (Hazan & Shaver, 1987; Kirkpatrick & Davis, 1994); and they report greater commitment to and trust in their dating partners (Brennan & Shaver, 1995; Simpson, 1990) and their spouses (Feeney, 1994; Fuller & Fincham, 1995; Kobak & Hazan, 1991).

In line with 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, have found that less securely 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, more 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, more avoidant parents report feeling less emotionally close to their first newborn child merely 2 weeks after birth (Wilson, Rholes, Simpson, & Tran, 2007), and more avoidant mothers are less emotionally supportive of their preschooler children, adopting a more detached, controlling, or instrumentally focused mode of relating to them (Crewell & Feldman, 1988, 1991; Rholes, Simpson, & Blakely, 1995).

Furthermore, mothers classified as secure on the Adult Attachment Interview (who probably received greater warmth and contingent care from their own parents) are more sensitive to the needs of their children and are more supportive of them (see Belsky, 2005a; Hesse, Chapter 25, this volume; van Ijzendoorn, 1995b). Specifically, greater attachment security is associated with more warmth and appropriate structuring of learning tasks by both fathers and mothers (Adam, Gunnar, & Tannaka, 2004; Cohn, Cowan, Cowan, & Pearson, 1992), greater emotional support in different situations (Crewell & Feldman, 1998, 1991), less negativity (Adam et al., 2004; Slade, Belsky, Aber, & Phelps, 1999), and greater awareness of children's needs (Das Eiden, Teti, & Corns, 1995).

The Chisholm Model

Chisholm (1993, 1996, 1999) has proposed a slightly revised and expanded model of alternate reproductive strategies—one that addresses the life history tradeoff of immediate versus delayed reproduction. Chisholm (1993) claims that local mortality rates are one of the critical environmental cues that shunt people down different developmental and reproductive pathways. According to bet-hedging theory (Horn & Rubenstein, 1984; Promislow & Harvey, 1990), when mortality rates are high in a local area, the optimal reproductive strategy is to mate early so that current fertility is maximized. When mortality rates are low, the best strategy may be deferred, long-term reproduction in which fewer progeny are given more intensive care. In abundant and safe environments that signal longer life expectancies, therefore, a delayed/high-investment reproductive strategy should increase the total number of descendants over multiple generations by minimizing the variance of surviving offspring within each generation. This, in turn, should decrease the likelihood that an entire generation will fail to reproduce.

High mortality rates, which should have been a barometer of the difficulty of local environments, typically should have been associated with poorer caregiving in the EEA. Chisholm (1993, 1996) claims that parental indifference or insensitivity should have been a valid cue of local mortality rates, motivating children to develop avoidant working models and behaviors that would have been better suited to increasing fitness in such arduous environments. Low mortality rates, which should have signaled more hospitable environments, should have been associated with better, more attentive caregiving. Sensitive parenting, in other words, should have conveyed to children that premature death was less likely, resulting in more secure working models and behaviors that might have enhanced fitness in benign environments.

In addition, Chisholm (1999) proposes another psychological mediator linking childhood experience and reproductive strategies: time preference. Time preference, which is associated with delay-of-gratification tendencies, reflects the degree to which individuals prefer to—or believe they will achieve—their desires now (immediately) versus later (in the future). Individuals raised in dangerous
or uncertain environments in which waiting for rewards may result in leaving no descendants should prefer immediate payoffs, even if delayed ones may be superior (Wilson & Daly, 2005).

Chisholm (1996) proposes that there were two parent-based threats to the survival and growth of children in the EEA: (1) parents' inability to invest in offspring, and (2) their unwillingness to do so. He contends that children and adolescents have evolved psychological mechanisms to detect and respond to these different forms of threat. Young infants are in fact fairly skilled observers of their parents' moods and motivations (Cohn & Tronick, 1983), and they are aware of others' intentions early in life (Woodward, Sommerville, & Guajardo, 2001). According to Chisholm's model and also in line with Belsky and colleagues' (1991) theorizing, the secure attachment pattern is a facultative adaptation to parents' psychological and parenting orientations, particularly to their ability and willingness to provide high investment. The anxious-avoidant attachment pattern, on the other hand, is an adaptation to parents' unwillingness to invest (regardless of their ability), whereas the anxious-ambivalent pattern is an adaptation to parents' inability to invest. The model proposes that warm-sensitive caregiving is a good indicator of parents' ability and willingness to invest, that cold/rejecting caregiving signals parents' unwillingness to invest, and that inconsistent/unpredictable caregiving conveys parents' inability to invest.

Building on the Belsky and colleagues model, Chisholm (1996) suggests how each of the three attachment patterns in children should map on to distinct reproductive strategies—something that Belsky and colleagues (1991) did vis-à-vis the secure versus insecure attachment distinction, and that Belsky (1997, 1999) did vis-à-vis all three primary attachment patterns. During childhood, secure individuals should maximize long-term learning to enhance their overall developmental quality, which explains why securely attached children typically grow faster than do insecure children in high-risk samples (Valenzuela, 1990) and why they display more advanced cognitive-perceptual and socioemotional skills earlier in development (Belsky & Cassidy, 1994; Straus, 1988). When parents are both able and willing to invest, and rearing environments are nonthreatening, greater effort can be allocated to long-term developmental quality and hence to future reproductive potential. Therefore, consistent with Belsky and colleagues' quality trajectory framework, more secure adults seek long-term mates, are able and willing parents, invest heavily in their children, and provide more sensitive and responsive care, all in the service of enhancing the phenotypic quality of their children.

Because avoidantly attached children have harsh and rejecting parents who force them to become independent at an early age, avoidant children must allocate resources differently. When parents are unwilling to invest in local environments are threatening, less effort and fewer resources can be devoted to physical growth. Effort and resources must be funneled to immediate reproduction, which accelerates sexual maturation. Consequently, more avoidant adults have shorter romantic relationships, are less willing to invest in children, allot more time and energy to mating effort, and feel less close to their children, all of which should increase offspring quantity.

Whereas Belsky and colleagues (1991) linked unsupportive rearing and insecure attachment patterns in general to accelerated pubertal development, Chisholm (1996) developed intriguing ideas about anxious-ambivalent individuals (see also Belsky, 1997, 1999). Chisholm believes that anxious-ambivalent children should channel more effort toward early sexual maturity (see also Belsky et al., 1991) while attempting to extract greater investment from their negligent or underinvolved caregivers (see also Cassidy & Berlin, 1994). According to Chisholm's LHT, when parents are willing but unable to invest, children should try to obtain as many resources as they can, funneling most of them to earlier reproduction. This helps to explain why anxious-ambivalent individuals are so irritable, demanding, and hypervigilant about gaining and maintaining time and attention from their caregivers, including their romantic partners (Cassidy & Berlin, 1994; Kuncz & Shaver, 1994). It might also explain why more ambivalently attached adults experience rapid and extreme sexual attraction to prospective mates (Hagan & Shaver, 1987). According to both Chisholm (1996) and Belsky and colleagues (1991), such adults should engage in short-term mating, want to but perhaps not be fully able to invest in children, and hence behave inconsistently toward them. Belsky (1997, 1999), on the other hand, has proposed that anxious ambivalence may reflect an evolved "helper-at-the-nest" reproductive strategy in which parenting effort is directed toward kin (siblings), particularly when local conditions demand more caregiving than parents can provide. However, no evidence consistent with such thinking has emerged to date.
Several additional findings are consistent with Chisholm's (1996, 1999) theorizing. As life expectancy declines in a local area, the probability that women will reproduce by age 30 increases (Wilson & Daly, 1997). Similarly, teen mothers who expect to die at a younger age are more likely to become mothers at an earlier age (Johns, 2003). These findings are consistent with Geronimus's (1996) “weathering hypothesis,” which proposes that early birth is a strategic response to the rapid decline in health among women in their 30s and 40s. In addition, meta-analytic research has revealed that when a mother experiences the loss of a loved one through death and the loss remains emotionally “unresolved,” the probability of her offspring developing a disorganized attachment pattern increases (van IJzendoorn, 1995a). These findings highlight the value of treating local mortality rates as a powerful cue in the development of alternate reproductive strategies.

The Belsky et al. and Chisholm models have both played important roles in getting scholars to think more deeply about how and why early experiences shape subsequent development—something that had been taken for granted by many developmental psychologists. Both models, however, could be 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 (see Gangestad & Simpson, 2000). Many of these factors have not been incorporated into current lifespan attachment models. One might pose the question, for example, whether secure individuals are better able than insecure individuals to attract partners who have higher mate value. Second, current models are not sufficiently sensitive to the different roles that men and women assume in reproduction (Buss & Schmitt, 1993; Geary, 2005; Hinde, 1991). The fact that women must make greater initial investments in their offspring than men do should influence how each gender makes reproductive decisions and the mating strategies they ultimately adopt (Hinde, 1984; Trivers, 1972). Sex-differentiating factors are not addressed by current lifespan attachment models. For example, relative to males, do females require stronger “doses” of poor or noncontingent early care to launch them down short-term, quantity-focused reproductive pathways? Third, evidence of pubertal timing effects in boys is absent. If future well-conducted studies fail to find theoretically meaningful pubertal timing effects for boys, the Belsky and colleagues and Chisholm models will obviously require revision. It is possible that the reproductive strategies of human females may be more sensitive to environmental inputs than those of human males are (cf. Gangestad & Simpson, 2000). 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 Ellis Model

Melding ideas from Belsky and colleagues (1991), Draper and Harpending (1982), and parental investment theory (Trivers, 1972). Ellis and colleagues (1999; Ellis & Garber, 2000) hypothesize that fathers may assume a special role in the development of girls' reproductive strategies. Belsky and colleagues viewed early father absence as a marker of stress in the family of origin and appreciated the influence of the quality of mothering and fathering. Ellis (2004), on the other hand, claims that father absence or stepfather presence may serve as a particularly important paternal investment cue signaling low, unpredictable, or changing levels of paternal investment within 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 (Campbell & Udry, 1995; Ellis & Garber, 2000; Ellis et al., 1999; Hetherington & Kelly, 2002; Moffitt et al., 1992; Rowe, 2000; Wierson et al., 1993) and in retrospective studies of adults (Doughty & Rodgers, 2000; Hetherington, 2002; Jones, Leek, McLovl, & Wood, 1972; Jorm et al., 2004; Kiernan & Holmes, 1997; Quillan, 2003; Romans et al., 2001; Surbecy, 1992). Similar effects, however, have not been found in African American samples (Campbell & Udry, 1995; Rowe, 2000).

Additional work has shown that the earlier father absence occurs in a child's life (especially within the first 5 years), the greater effect it has on the speed of female pubertal development (Ellis & Garber, 2000; Jones et al., 1972; Quillan, 2003; Surbecy, 1992). Stepfather presence may also affect pubertal timing, perhaps even accounting for some of the father absence effects (see Ellis, 2004). Supporting this view is the observation that great-
er conflict between the mother and stepfather, combined with earlier stepfather presence in the home, seems to be particularly 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 in the first 5 years of life and the more fathers have positive/affective interactions with their daughters at age 5.

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

The Hazan/Zeifman and Kirkpatrick Models

Scholars have also sought to explain the nature and strength of adult romantic pair bonds from a life history/attachment perspective. Hazan and Zeifman (1999; Zeifman & Hazan, 1997; see also Zeifman & Hazan, Chapter 20, this volume), for example, suggest that adult romantic relationships are an instantiation of attachment relationships formed earlier in life. They note numerous similarities between childhood attachment to caregivers and adult attachment to close peers and romantic partners (see also Shaver et al., 1988). For example, infants and adults display very 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 quite similarly when seeking close contact, physical intimacy, and affection from their attachment figures. Parent–child and adult–adult attachment relationships also pass through similar sets 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 that mates can provide better mutual support. Pair bonding is thus believed 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). More pair-bonded partners should also contribute to their own reproductive success by providing one another with greater support, which tends to be associated with better long-term physical and mental health and more regular ovulation patterns (see Zeifman & Hazan, 1997).

Partially in response to this model, Kirkpatrick (1998) claims that adult attachment styles evolved to enhance reproductive fitness in light of 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 coopted during evolutionary history to cement romantic pair bonds in adulthood, and that (similar to the Belsky and colleagues and Chisholm models) adult attachment styles primarily reflect evolved reproductive strategies.

One of the principal life history tradeoffs involves allocating time and energy to mating effort more or less than to parenting effort. Kirkpatrick (1998) argues 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 “mechanisms” for choosing the best mating strategy, given the nature of early childhood experiences and the quality of early parental investment as discussed by Belsky and colleagues (1991). Individuals who receive consistently sensitive and responsive parenting should develop secure working models and thus should adopt long-term, committed mating strategies. These individuals should also develop greater trust and intimacy in their relationships (Simpson, 1990) and should fall in love rather easily with partners who tend to have higher mate value (Hazan & Shaver, 1987), which they do. More avoidant individuals, in contrast, should be involved in less committed relationships, should pursue short-term mating strategies, and should have more unrestricted sociosexual orientations, which they do (see Simpson, Wilson, & Winterheld, 2004). And more anxious-ambivalent persons should desire and want to pursue long-term
mating strategies, but their strong desire to be attractive to and merge with their romantic partners may result in short-term sexual relationships in which they eventually drive partners away (see Kirkpatrick, 1998). For these reasons, Kirkpatrick believes that features of the caregiving system—especially love operating as a "commitment device" (Frank, 1988)—could have been coopted to bind and stabilize long-term romantic pair bonds.

UNRESOLVED ISSUES
AND PROMISING DIRECTIONS

Several unresolved issues and promising directions for future research exist, only a few of which can be covered here to complement some of the questions and hypotheses raised in this chapter. Two of the most perplexing questions in the attachment field center on (1) why maternal sensitivity accounts for only a portion of the variance in children's attachment status, and (2) why the intergenerational transmission of attachment patterns is not stronger than it is (see also van Ijzendoorn & Bakermans-Kranenburg, 1997). Possible solutions to these puzzles might be achieved through applications of LHT. Applying bet-hedging logic, Belsky (1997, 2000, 2005b) has theorized that children should differ in their susceptibility to parental influence (see also Boyce & Ellis, 2005). Experimental evidence relevant to this prediction focusing on the influence of maternal sensitivity on attachment security has recently been reported (Velderman, Bakermans-Kranenburg, Juffer, & van Ijzendoorn, 2006). Also relevant are twin studies showing that nonshared environmental influences explain much more of the variation underlying most traits and behaviors than shared environmental influences do (Bouchard, 2004; Turkheimer & Waldron, 2000), and that attachment security is not heritable (Bokhorst et al., 2003). Belsky (2000, 2005b) suggests that differential susceptibility might be adaptive for parents, children, and their siblings if a parent's attempt to "prepare" his or her children for the future environment could be 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 initially expected (Belsky, 2005a).

Less-than-perfect intergenerational transmission rates also raise intriguing questions about the possible "time span of influence" on present and future decision making. 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, with little consideration of the possible impact of grandparents, great-grandparents, etc.). The concept of "intergenerational phenotypic inertia" (see Kurawa, 2005), however, suggests that some forms of influence may endure over 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 typically place greater diagnostic weight on conditions in the current (immediate) environment when allocating life history resources than on cues signaling the environments in which their parents, their grandparents, or more distant relatives lived, even if past environments were stable over multiple generations. There may be cases, however, when looking back only one generation may not be the best way to interpret or model intergenerational transmission processes, particularly when environments are very stable across several generations.

This raises another critical 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). Indeed, the strategic pluralism model (Gangestad & Simpson, 2000) proposes that human females may have 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, which still characterize the current world and perhaps characterize the EEA, women should place more weight on men's viability attributes so that the "good genes" of such mates may 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 with different attachment histories and styles may evaluate, calibrate, or apply each mate dimension somewhat differently. This returns
us to an issue raised earlier about the mate value of relationship partners. Highly avoidant women, for instance, may expect and require less paternal investment in light of their independence and self-reliance, and due to their mistrust of others, they may want less. Highly anxious women, in contrast, may expect and demand greater investment, given their chronic concerns about relationship loss and abandonment.

Finally, epigenetics research holds the promise of advancing our understanding of intergenerational attachment issues in major ways. Recent animal work, for example, has shown that maternal grooming of newborn female rat pups not only calibrates their stress response system when they are adults and raise their own offspring. Through nongenetic mechanisms, such care also influences the development of the grandoffspring of the original grooming mother (see Cameron et al., 2005). These findings are important because they partially complete the attachment/mothering intergenerational cycle. This research calls attention to the fact 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 via nongenetic means. This evidence raises additional intriguing questions about recent research on gene–environment interactions (see Caspi et al., 2002). This work, which supports the notion of differential susceptibility to parental influence, shows that the impact of rearing effects (e.g., child maltreatment) on the development of antisocial behavior varies as a function of 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 the development of antisocial behavior.

CONCLUSIONS

At its (secure) base, 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 shed light on how attachment patterns across the lifespan—including adult romantic attachment styles—may have evolved to increase reproductive fitness. These new 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 plays perhaps the leading role in shaping attachment security in children (Belsky, 2007). Traditionally, attachment theorists and researchers have focused on how these processes work. Recent applications of LHT within attachment theory have begun to rectify this deficiency in the original theory, directing attention to questions concerning both ultimate and proximate causation. These recent theoretical advances are also important because they suggest that adult attachment styles may 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, alternate reproductive strategies, not just satisfaction and happiness in close relationships.

In the future, attachment scholars would be well advised to base more of their thinking on 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 much of developmental and social psychology in particular, especially those fields that focus on close interpersonal relationships. We strongly advocate treading the intellectual path first paved by Darwin and then 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 LHT—have a tremendous amount to offer scholars interested in attachment phenomena across the lifespan. 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.

NOTES

1. These are only some of the major middle-level evolutionary theories that have been developed. Others include host–parasite coevolution theory (Hamilton & Zuk, 1982; Tooby, 1982) and intragenomic conflict theory (Trivers, 1977).
2. Main and Solomon (1990) identified a fourth attachment pattern in children, labeled “disorganized/disoriented.” These children do not have a clear, coherent strategy for managing negative affect, frequently intermixing anxious-avoidant and anxious-ambivalent behavioral tactics with bizarre ones. This pattern, which has the lowest base rate, tends to be witnessed when caregivers are abusive, neglected, or emotionally disturbed (see Lyons-Ruth & Jacobvitz, Chapter 28, this volume).

3. These precipitating conditions may interact in interesting ways. For example, males in most polygynous species have more variable reproductive success than females do (Trivers, 1985). In our ancestral past, nearly all fertile females reproduced and had approximately the same number of children, whereas some males had large numbers of children and others failed to reproduce. Trivers and Willard (1973) have proposed that when environmental resources are limited, daughters should receive more parental investment than sons. Most daughters will eventually bear children if environmental conditions are not too severe, whereas sons who cannot amass resources or display evidence of their fitness may never attract mates. When environmental conditions are better, however, sons should receive greater investment than daughters, because the most reproductively successful males should, on average, propagate their parenting capacity more extensively than their daughters. This reasoning suggests that when environmental conditions are harsh, the pattern of parental investment may lead to more daughters than sons being securely attached, whereas the reverse may be true when environmental conditions are favorable.

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