1

An Evolutionary Life History Perspective on Personality and Mating Strategies

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An understanding of personality—which includes broader personality traits such as the Big Five as well as stable individual differences such as attachment orientations—and its origins is relevant not only to psychology but also to all fields in the social, behavioral, and life sciences. The reason is simple: The way in which individuals perceive, process, interpret, and remember daily events in their lives is filtered through their schemas (working models) of the social world, many of which have developed in conjunction with their most salient traits. Since the early 1990s, evolutionary scientists have attempted to discern how and why certain personality traits and associated individual differences emerge and develop in different people across their lives. Many of the key ideas and findings underlying this work, however, have not been integrated into mainstream personality theory and research. As a result, the general field of personality has not taken full advantage of one of the most powerful and influential sets of ideas in the biological and life sciences—the modern evolutionary perspective (for a recent summary of this broad perspective, see Buss, 2016).

From an evolutionary standpoint, how can one determine whether, how, and why certain personality traits—or sets of correlated traits and individual differences—develop in certain people? One way to do so is to ask a specific type of "why" question. Consider the life trajectories of two individuals, Tim and John, both of whom are in their early 20s.

Tim was raised in a stable, relatively stress-free environment as a child where he received consistently supportive care from his parents. Partly

in response to his early environment, he developed a secure attachment orientation to his parents, learned he could trust others, and developed close, emotionally intimate relationships with his friends and a few romantic partners in adolescence. As a young adult, Tim is an agreeable, introverted, and somewhat inhibited non-risk taker who is good at regulating his emotions and behaviors. With respect to his mating tendencies, Tim has a restricted (slow) sociosexual orientation, preferring to forge deeper and more committed emotional involvements with select romantic partners.

John, in contrast, has a very different background. During childhood, John was raised in an unstable, rather stressful environment where he received less supportive and more erratic care from his parents. Partially in response to this upbringing, he developed an insecure attachment orientation to his parents, learned he could not trust others completely and had to seize opportunities when they arose, and developed less emotionally intimate relationships with most of his friends and many different romantic partners in adolescence. As a young adult, John is a disagreeable, extraverted, and uninhibited risk-taker who has difficulty regulating his behaviors and emotions. In terms of his mating tendencies, John has an unrestricted (fast) sociosexual orientation, preferring to have more casual sexual relationships with a series of different romantic partners.

How and why did Tim and John develop these different trait configurations? Behavioral geneticists note that they stem at least partly from the genes that Tim and John inherited from each of their parents. From an evolutionary perspective, however, this explanation is incomplete because it does not fully explain why Tim's and John's parents have the unique personality profiles they do, nor does it explain the kinds of environmental inputs that were required for the expression of these traits. The key to conceptualizing personality from an evolutionary standpoint is to recognize that specific personality traits and individual difference scores are not merely the outcome of random reshuffling of genes from generation to generation. Instead, certain clusters of traits may be *adaptive* in that they conferred survival and reproductive benefits to the individuals who possessed them during evolutionary history, especially when they were enacted in certain types of environments. As we elaborate later in the chapter, several evolutionary processes could generate these outcomes, including the heritability of individual differences that are selectively neutral, those that are maintained by mutation-selection balance, or those that are balanced by environmental heterogeneity (Penke, Denissen, & Miller, 2007).

But if it was evolutionarily advantageous for Tim and John to develop these specific traits, why are they so different? The main reason, according to evolutionary thinking, is that scoring high, moderate, or low on any given trait is typically associated with both benefits and costs (Nettle, 2006). For example, Tim's inclination to be a restricted individual who is agreeable,

introverted, inhibited, and well regulated may have resulted in certain adaptive benefits in our evolutionary past. This cluster of traits, for instance, may have better enabled him to establish more trusting friendships, to be well liked by others, and to attract a highly committed and caring long-term mate. These traits, on the flip side, may also have carried some evolutionary costs. For example, they might motivate Tim to be less daring and take fewer risks than John, leading Tim to miss out on opportunities that might elevate his social status or mating success with multiple partners. All trait clusters, therefore, are associated with certain *trade-offs*, and evolutionary approaches articulate how and why certain trade-offs tend to be made by different people across their lives.

While most personality traits are partially heritable (Bouchard, 2004), an individual's score on any trait—high, moderate, or low—is not pre-ordained from birth. Rather, it is shaped in part by the environmental events that he or she encounters during social development. When Tim was born, for instance, he was not bound to be agreeable, harm-avoidant, emotionally stable, and have a restricted (slow) sociosexual orientation. Instead, he was prepared to evaluate and react to his developmental environment in ways that, in many situations, would have increased his reproductive success in evolutionary environments. Partly in response to certain early environmental cues, Tim and John both developed trait profiles that were well adapted to the demands and needs of the environments in which they were raised, with their genetic make-up being influential but by no means deterministic. In addition, Tim and John did not consciously "decide" to enact their unique personality profiles. Instead, adaptive psychological mechanisms shaped by prior selection pressures motivated them to display the personality profile that "felt natural" to them and was best suited to the particular features of their social upbringing.

The primary goal of this chapter is to elucidate why and how the incorporation of more modern evolutionary thinking into the field of personality can generate novel, important insights into how and why certain personality traits—and variability in those traits—exist. We apply life history theory (LHT) as an explanatory evolutionary framework because it is an overarching metatheory that links several major middle-level evolutionary theories (Del Giudice, Gangestad, & Kaplan, 2016), it has generated compelling empirical support in many different species (Ellis, Figueredo, Brumbach, & Schlomer, 2009), and it is well suited for explaining how and why certain mating orientations develop in certain individuals across social development (Simpson & Belsky, 2016). The chapter has five sections. In the first section, we describe some key features of the evolutionary approach and discuss how it can extend and enrich our understanding of personality traits. In the second section, we review evolutionary theories that explain why variation exists in all major traits and stable individual differences. In doing so, we

highlight the core tenets of the evolutionary model of social development (Belsky, 1997; Belsky, Steinberg, & Draper, 1991), which provides an ontogenetic (developmental) account of the early-life conditions that should result in two prototypical reproductive "strategies," each of which should have distinct personality trait correlates. In the third section, we summarize recent findings from the Minnesota Longitudinal Study of Risk and Adaptation (MLSRA; Sroufe, Egeland, Carlson, & Collins, 2005), a project that has followed approximately 180 people from before birth into adulthood. In particular, we test whether certain types of early-life environments—especially exposure to less stressful, more predictable ones—prospectively predict the development of restricted (slow) sociosexual orientations in early adulthood through two theory-relevant developmental mediators: the quality of care received early in life and attachment representations of parents. In the fourth section, we discuss the main personality correlates associated with restricted (slow) and unrestricted (fast) sociosexual orientations and indicate how these specific clusters of traits should facilitate the enactment of these reproductive strategies. Finally, in the last section, we consider alternative evolutionary models of individual differences in personality and the possible role of culture in life history models.

KEY FEATURES OF AN EVOLUTIONARY APPROACH

Charles Darwin (1859, 1871/1981) conjectured that natural selection shapes not only morphological features (e.g., the intricate design of a bird's wings, the specialized features of a human's eyes) but psychological and behavioral tendencies in all species as well. Bats, for example, have specialized brain mechanisms capable of detecting the sonar-like sounds emitted by prey, which allow them to locate and successfully hunt prey while flying rapidly in total darkness. Monkeys have specially designed brain circuits for binocular color vision, which allow them to better estimate distances while swinging between branches as they ascertain the ripeness of fruit in different trees. These are only two of many examples that illustrate how different mental mechanisms have evolved to meet the demands of the specific environments and habitats for a given species.

All living animals, according to evolutionary thinking, have brains and bodies that are fairly well equipped to respond adaptively, on average, to their environments—that is, to behave in ways that typically match the unique demands of the environments in which their ancestors evolved, resulting in greater overall reproductive fitness. Reproductive fitness reflects the extent to which an individual's alleles, whether they are passed on through direct reproduction or through support of one's biological relatives, are represented in future generations (Tooby & Cosmides, 1992). Some adaptations are shared by different species through common descent, some are shared because of

exposure to similar ecological conditions, and some are specially designed to solve the unique problems routinely encountered by a given species across its protracted evolutionary history (see Simpson & Campbell, 2016).

This evolutionary logic, of course, applies to humans as well. Natural selection has also crafted many complex human traits, such as those that generate language, emotion, mating behavior, parenting, and a host of others. Thus, just as human morphological features—eyes, opposable thumbs, larynxes, and livers—were shaped by evolutionary pressures, humans also inherited evolved brain mechanisms that are well designed to solve the major, recurrent problems that affected survival and reproduction in our ancestral past. To complement the larynx, for example, humans also have evolved brain mechanisms that allow them to learn to communicate and use complex language automatically and with a remarkable degree of proficiency. Despite the fact that specific words and sounds differ from culture to culture, all human languages share the same basic universal structure, which reveal evolved human mechanisms for language (Pinker, 1994).

From evolutionary perspectives, "Why" questions regarding the origins of specific traits and behaviors can be asked at four distinct yet compatible levels of analysis—adaptive function, evolutionary history, ontogenetic development, and proximate causation (see Kenrick, Griskevicius, Neuberg, & Schaller, 2010; Simpson & Gangestad, 2001; Tinbergen, 1963). To illustrate this key point, consider the following question: "Why are dominance displays more likely to be made by male chimpanzees than female chimpanzees?" This specific "why" question can be addressed at all four levels of analysis, with explanations at one level typically complementing those at other levels. Although most evolutionary scientists are primarily interested in the first level (adaptive function), all four levels are equally important and informative:

1. *Functional* (ultimate) explanations address the *ultimate adaptive* purpose(s) of a specific trait or behavior. A functional explanation, for instance, might focus on associations between dominance and reproductive success in male versus female chimpanzees, noting that dominance tends to be more relevant to reproductive success in males than in females.

2. *Historical* (phylogenetic) explanations focus on the ancestral origins of a specific trait or behavior in relation to other species on the phylogenetic tree. Researchers who pursue this approach might, for instance, view sex differences in chimpanzee dominance in relation to other primate species and increasingly more biologically distant relatives, noting that males tend to be larger and more competitive in most mammalian species (see Eastwick, 2009, and Fraley, Brumbaugh, & Marks, 2005, for applications of this approach).

3. *Developmental* (ontogenetic) explanations, which we showcase in this chapter, examine the lifespan-specific inputs that sensitize an organism to particular environmental cues, which influence its later development. A developmental explanation, for example, might note that maturing male chimpanzees experience

pronounced hormonal changes during adolescence, making them more prone to displaying dominance-related behaviors than is true of females.

4. *Proximate* explanations identify the immediate situational events that trigger (turn on) and curtail (turn off) the display of a specific trait or behavior. A proximate explanation, for example, might reveal that displays of male dominance are typically triggered by threats from other males and that responses to other males' displays are facilitated by higher levels of circulating testosterone.

Sometimes there is a clear connection between the different levels of analysis with respect to a specific trait or behavior. For example, the four types of answers to the question "Why do mothers nurse their young?" are clearly related: a *functional* explanation—infants who are nursed and given better nourishment are more likely to survive; a *historical* explanation—all mammalian females nurse their young, based on the way in which mammals reproduce; a *developmental* explanation—pregnancy produces hormonal and other changes in the body that facilitate lactation; and a *proximate* explanation—suckling the nipple releases mothers' milk. In other cases, however, direct connections between the four levels are less apparent. Consider the question "Why do birds migrate each year?" The *proximate* explanation is that migration occurs when days become shorter, with the amount of sunlight each day being the proximate cue that stimulates migration. The *functional* explanation, however, is that migration increases a bird's chances of survival because the distribution of good, abundant food varies across the seasons in different geographical locations. Birds, of course, do not understand the direct associations between day length, food, and survival. With respect to many evolved human traits and behaviors, most evolutionary theorists do *not* assume that the ties between proximate, developmental, historical, and functional levels of analysis are either direct or obvious to most humans (Alcock & Crawford, 2008).

The majority of evolutionary approaches focus chiefly on "why" questions at the functional level, which once again address the ultimate adaptive purpose(s) of a given trait or behavior. Most evolutionary researchers, however, do not limit their attention to only this one level of analysis. Indeed, part of the power of an evolutionary approach comes from *integrating* research questions and answers across the four levels of analysis, which often results in a more complete, nuanced understanding of a given trait or behavior. Let's return to Tim, who is an agreeable, introverted, rather inhibited, and emotionally stable person with a restricted (slow) sociosexual orientation. To fully understand why Tim has this specific set of traits, we must view him at all four levels of analysis: (1) *Functional*: What might have been the evolutionarily adaptive benefits to Tim (as well as John, his extraverted, risk-taking, unrestricted counterpart) of possessing these specific traits?; (2) *Historical*: Do other mammalian species exhibit this type of personality

trait/behavior profile and, if so, how?; (3) *Developmental*: Are there particular experiences during childhood that partially explain why Tim (as well as John) developed the unique traits they did in adulthood?; and (4) *Proximate*: What are the current environmental stimuli that motivate Tim (and John) to behave in line with their unique constellation of traits most directly and strongly? By asking "why" questions at all four levels, we obtain a much richer and more complete understanding of how and why Tim and John became the unique persons they now are.

LIFE HISTORY THEORY AND PERSONALITY VARIATION

From an evolutionary life history standpoint, why would it have been adaptive in evolutionary history for there to be variability in certain personality traits or behaviors? To answer this question, we consider three important factors that can lead individuals (organisms) to adopt specific personality profiles in response to three types of environmental factors: (1) The frequency of other personality "types" in the local environment (e.g., Are a person's traits/behaviors similar to or different from those around him or her?); (2) Mortality Level (e.g., Is the local environment a dangerous or a safe place in which to live?); and (3) Parental Investment (e.g., Is the quality/amount of parental investment high or low across social development?). To help understand how these factors influence personality, we first provide an overview of LHT, which is a central underlying framework for understanding trade-offs from an evolutionary perspective.

LHT (Charnov, 1993; Del Giudice et al., 2016; Kaplan & Gangestad, 2005) focuses on how traits emerge in response to specific life events encountered at different points of development. Because time, effort, and resources are inherently limited, all organisms must make *trade-offs* in how they allocate their time, effort, and resources at each phase of their lives. Given these constraints, organisms cannot maximize each major component that impacts their overall reproductive fitness simultaneously (i.e., survival, reproduction, caring for offspring and kin). According to LHT, therefore, all organisms must prioritize the specific life-domain(s) into which current resources are allocated. LHT, therefore, focuses on the selection pressures in our ancestral past that should have affected when, and the environmental conditions under which, individuals devoted time, energy, and resources to physical development, growth, reproduction, and parenting.

Individuals must negotiate three fundamental trade-offs when "deciding" (nonconsciously) how to allocate their limited time, energy, and resources at different points of development: (1) whether to invest more in current (immediate) reproduction OR in future (delayed) reproduction; (2) whether to invest more in higher quantity OR in higher quality offspring; and (3) whether to invest more in mating OR in parenting. Individuals historically could not invest

large amounts of time, energy, or resources to one side of any of these trade-offs without investing less in the other side. Consider the trade-off between current (immediate) reproduction and future (delayed) reproduction. Investing heavily in current reproduction historically implied that a person *cannot* invest as much in future reproduction. In modern Western societies, for example, people who have children as teenagers often do not have the time, money, or energy to get more or better education or valuable job experiences, which might have situated them better for finding mates and having children later in life.

It is important to reemphasize that organisms (including people) are often not consciously aware of making these trade-offs. Instead, their motivational and emotional systems have evolved to respond in specific ways to specific environmental cues (R. Wright, 1994). Some environments nonconsciously motivate certain individuals to prefer one trade-off decision, whereas other environments nonconsciously motivate other individuals to make a different decision. We now review three types of environmental factors that, according to evolutionary thinking, may contribute to the development of specific personality traits or profiles. We direct most of our attention to the third one—Belsky and colleagues' (1991; Belsky, 1997) evolutionary model of social development.

Personality as a Function of the Frequency of Other Personalities

One environmental feature that can shape personality traits is the traits of other people, especially those who are or could become competitors. When traits are viewed in social isolation (i.e., one person living alone on an island), having a specific constellation of traits is not necessarily "good" or "bad" in an evolutionary sense. But when those traits are viewed *in relation to* the distribution of traits enacted by other people in the same environment, traits can differ in their adaptive value. It may be more adaptive for an individual to remain open to novel experiences and take more risks, for instance, when most others in the local environment are highly risk-averse. Greater openness and risk-taking might allow an individual to find (or create) novel solutions to problems associated with survival, mating, or parenting, which may give her or him a fitness advantage over those who are risk-averse. Greater openness, however, should decline in its fitness value if most people in the local environment are or become risk-takers. According to frequency-dependency models (e.g., Gangestad & Simpson, 1990), therefore, the adaptive value of a given trait depends on its value and base-rate within the local population.

Another critical insight of related evolutionary models is that there are likely to be trade-offs depending on whether individuals score high or low

on certain traits. For example, scoring high or low on each of the Big Five traits could have yielded both benefits *and* costs in evolutionary history (MacDonald, 1995; Nettle, 2006). Greater agreeableness, for instance, may have generated several evolutionary benefits by helping these individuals to be more aware of what others were thinking and feeling, to form better and more committed relationships, and to forge stronger social networks with coalition partners. At the same time, however, high agreeableness may also have produced certain systematic costs, such as a greater likelihood of being swindled or failing to promote and defend one's own self-interests in certain situations. Highly conscientious people might have benefited evolutionarily from paying greater attention to their health and other long-term fitness outcomes (thereby living longer), but they may also have engaged in obsessive thinking, rigid ways of doing tasks, and may have been less inclined to pursue certain short-term fitness benefits. People scoring higher on openness might have been more creative and better at attracting mates in evolutionary history, but they may also be more prone to psychoses and delusional thinking. Highly neurotic individuals may have been more vigilant to possible danger and more willing to compete with others for valuable resources in our evolutionary past, but might also have been more susceptible to depression, more stress-reactive, and less able to maintain stable relationships. And highly extraverted people might have had more mates, more social connections, and may have been more inclined to explore and take advantage of novel environments ancestrally, but they may also have been more vulnerable to physical injuries and unstable relationships (see Nettle, 2006, for more details).

Personality as a Function of Mortality Levels

Chisholm (1993, 1996, 1999) has proposed that life history trade-offs are also contingent on local mortality rates, which shunt individuals down different developmental and reproductive pathways. When mortality rates are high in a local area, the optimal reproductive strategy is to mate early so current fertility is maximized prior to a possible early death (Horn & Rubenstein, 1984; Promislow & Harvey, 1990). When mortality rates are low, on the other hand, the best strategy is deferred, long-term reproduction in which fewer children are given better and longer care. Thus, in resource-abundant, safe, and less stressful environments associated with longer life expectancies on average, a delayed/high investment reproductive strategy ought to increase the total number of descendants over many generations, primarily by minimizing the *variance* of surviving offspring in each generation. This, in turn, should decrease the likelihood that an entire generation of progeny fails to reproduce.

High mortality rates should have been a good barometer of the difficulty and danger of the local environment in evolutionary history (Chisholm,

1999), and they should have resulted in poorer, less invested parenting. Chisholm (1993, 1996) suggests that parental indifference or insensitivity may have functioned as a valid cue of local mortality rates, motivating children to develop appropriate traits and behaviors (e.g., greater aggression, less cooperation, less trust) that were better suited to increasing fitness in these difficult environments. Low mortality rates, which may have signaled more hospitable, less stressful environments, should have been associated with better caregiving. Sensitive parenting, therefore, may have conveyed to children that premature death was less likely, yielding different traits and behaviors (e.g., less aggression, more cooperation, more trust) that enhanced fitness in these more benign, resource-abundant environments.

In addition, Chisholm (1999) contends that time preference connects (mediates) early childhood experience with the enactment of different adult reproductive strategies. Time preference, which is closely tied to delay-of-gratification tendencies, reflects the degree to which individuals prefer or believe they will achieve their desires now (immediately) or later (in the future). Individuals raised in dangerous or unpredictable environments, in which waiting for rewards might result in leaving no descendants should prefer immediate payoffs, even if delayed ones could be superior (Wilson & Daly, 2005), and they do (Griskevicius et al., 2013).

Personality as a Function of Parental Investment

Inspired by LHT and research on father absence during childhood (e.g., Draper & Harpending, 1982), Belsky and his colleagues (1991) developed the first evolution-based lifespan model of human social and personality development. According to their evolutionary model of social development, the main evolutionary function of early social experience is to prepare children for the social and physical environments they are likely to inhabit across their lifetimes. The model focuses principally on the trade-off between offspring quantity and offspring quality. Certain types of information gleaned from the early environment should allow individuals (children) to adopt an appropriate reproductive strategy—one that, on average, would have increased their 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 more aggressive and less cooperative should have higher reproductive fitness as adults compared to those who do not to have these tendencies. Conversely, offspring raised in less stressful environments with abundant resources could increase their fitness by adopting a more co-operative, communal orientation toward others in adulthood.

As shown in Figure 1.1, the Belsky et al. (1991) model has five stages. It proposes that (a) early contextual factors in the family of origin (e.g., the

amount of stress, spousal harmony, financial resources) affect (b) early childrearing experiences (e.g., level of sensitive, supportive, and responsive caregiving). These experiences in turn affect (c) psychological and behavioral development (e.g., attachment orientations, trust, opportunism), which impact (d) somatic development (how quickly sexual maturation is reached) and eventually (e) the adoption of specific reproductive strategies (e.g., time of first sexual intercourse, stability of pair-bonds, quality of parental investment). Even though these stages are linked sequentially in the model, earlier stages can also statistically interact to predict later outcomes. Early contextual factors in the family of origin, for example, might interact with early childrearing experiences to predict the rate of somatic development.

Belsky et al. (1991) hypothesized that two developmental trajectories culminate in adulthood in two distinct reproductive strategies, which might either be on opposite ends of a single continuum or might be distinct alternate types. One strategy, shown on the left side of Figure 1.1, reflects a fast, 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 should increase the quantity of offspring. The second strategy, shown on the right of Figure 1.1, reflects a slow, long-term, investing orientation toward mating relationships in which sexual intercourse occurs later in life, romantic pair-bonds are more enduring, and parental investment is greater. This orientation should maximize offspring quality.

Growing evidence supports various sections of the Belsky et al. model (see Simpson & Belsky, 2008, 2016, for recent reviews). The one major exception is that adverse early-life experiences speed up reproductive timing of girls (i.e., age of menarche), but they do not affect the reproductive timing of boys. To date, the vast majority of the findings linking different stages of this model with each other have relied on cross-sectional or short-term longitudinal data. Very few studies have (1) followed individuals from before birth across their lives and (2) measured the "right" variables in the model at the proper developmental time points. In what follows, we report new findings that prospectively examined some of the key components of this model across the first 23 years of life in a unique longitudinal sample.

THE DEVELOPMENT OF MATING STRATEGIES: PROSPECTIVE LONGITUDINAL FINDINGS FROM THE MLSRA

According to Belsky et al.'s (1991) model of social and personality development, a slow (restricted) reproductive strategy is characterized by a slower pace of development and reproduction, which facilitates more

Developmental Pathways of Divergent Reproductive Strategies

FAST

Marital discord
High stress
Inadequate $ resources

Harsh, rejecting, insensitive
Inconsistent

Insecure attachment
Mistrustful internal
    working model
Opportunistic interpersonal
    orientation

Early maturation/ Puberty

Earlier sexual activity
Short-term, unstable pair bonds
Limited parental investment

A. Family Context

B. Child-rearing
Infancy/Early Childhood

C. Psychological/
Behavioral Development

D. Somatic Development

E. Reproductive Strategy

SLOW

Spousal harmony
Adequate $ resources

Sensitive, supportive, responsive
Positively affectionate

Secure attachment
Trusting internal working
    model
Reciprocally-rewarding
    interpersonal orientation

Later maturation/ Puberty

Later sexual activity
Long-term, enduring pair bonds
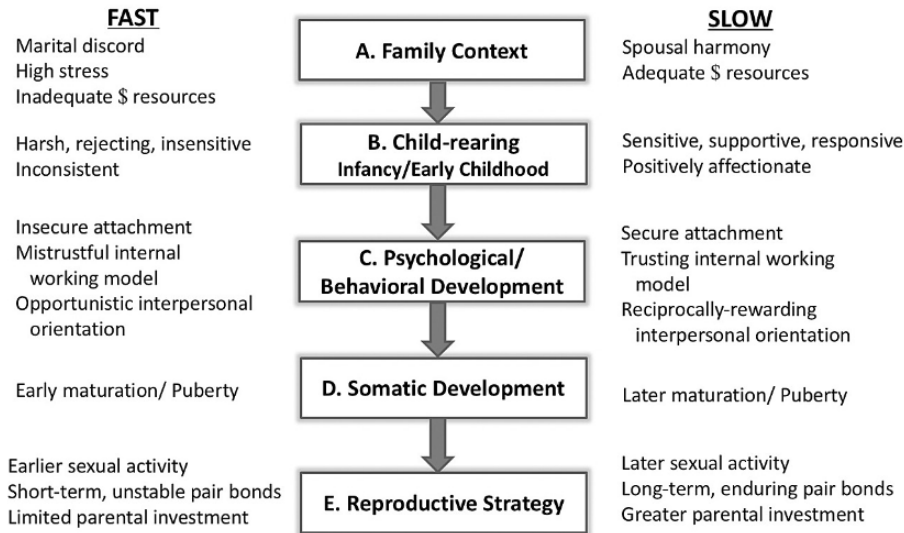Greater parental investment

Figure 1.1   Lifespan model of human social and personality development.

investment in fewer, but higher-quality, offspring. Conversely, a fast (unrestricted) reproductive strategy involves a faster pace of development and reproduction, resulting in more offspring but less investment in each one. Given these differences, slow strategists tend to invest more time and effort in maintaining long-term, committed relationships that facilitate more investment in fewer offspring, whereas fast strategists tend to invest more time and effort in pursuing multiple sexual partners and short-term mates and less in building long-term, committed relationships (Belsky et al., 1991). These patterns, of course, are also likely to be affected by the prevailing rules, norms, expectations, and customs that exist in a given culture.

Predictable, Harsh, and Unpredictable Conditions

As mentioned earlier, the adaptive value of a given life history strategy should depend on the environmental context in which it unfolds developmentally, such as the overall levels of morbidity and mortality (harshness) and the quality of parental care (Belsky et al., 1991; Kaplan & Gangestad, 2005; Simpson & Belsky, 2008, 2016). Recent developments in LHT have highlighted another key environmental feature: the extent to which the environment is predictable versus unpredictable (Ellis et al., 2009). Unpredictability is typically indexed by frequent changes within the family environment that directly affect parents and their children (Belsky,

Schlomer, & Ellis, 2012; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012; Szepsenwol, Simpson, Griskevicius, & Raby, 2015).

The costs and benefits of entering a long-term romantic relationship are particularly dependent on the extent to which the environment is predictable. In predictable environments parents can increase the survival and well-being of their children through strong biparental investment, which normally requires the formation and maintenance of a long-term, committed relationship. Taking the time to invest in long-term relationships that result in fewer but higher-quality offspring makes sense when individuals can be fairly certain their long-term investment will pay off. In unpredictable environments, however, such long-term investments can have catastrophic outcomes if environmental conditions took a turn-for-the-worse. Sudden increases in juvenile mortality rates, for example, could cause slow strategists to lose their entire investment very quickly. In these unstable, unpredictable environments, it makes more sense to pursue reproduction opportunities when they arise and have more offspring to improve the odds that some will survive to adulthood (Ellis et al., 2009). It might also be beneficial to diversify the genetic material of one's offspring by mating with different partners (i.e., bet hedging; Donaldson-Matasci, Lachmann, & Bergstrom, 2008). Fast strategies characterized by more unrestricted sociosexuality, therefore, should be more advantageous in unpredictable environments, whereas slow strategies and restricted sociosexuality ought to be more advantageous in more stable, predictable ones.

The Significance of the Early Environment

Because the adaptive value of reproductive strategies is partially dependent on the amount of harshness and predictability in the environment, the evolved psychobiological mechanisms that regulate these strategies should be sensitive to their unique cues. Indeed, associations between fast reproductive strategies and indicators of exposure to environmental harshness and/or unpredictability have been found at both the population level (e.g., Low, Hazel, Parker, & Welch, 2008; Walker et al., 2006) and the individual level (e.g., Kotchick, Shaffer, Forehand, & Miller, 2001). These associations reflect "strategic fine-tuning" not only in response to current (immediate) environmental conditions but also in response to exposure cues early in life that signal environmental harshness or unpredictability (Belsky et al., 1991; Ellis et al., 2012). Similar to other organisms, human developmental systems orient development based on cues signaling the nature of the environment in which the individual will most likely live (Del Giudice & Belsky, 2011; West-Eberhard, 2003), meaning that early rearing environments may have enduring effects on reproductive strategies, above and beyond current (immediate) environment effects.

Following this logic, exposure to more unpredictable early-life environments should promote the development of faster reproductive strategies (more unrestricted sociosexuality), whereas exposure to more predictable early environments should promote slower reproductive strategies (more restricted sociosexuality). Findings consistent with this prediction have been reported in a few prospective longitudinal studies. For example, experiencing a more predictable environment during the first years of life uniquely forecasts fewer sexual partners by age 15 (Belsky et al., 2012) and later age of first pregnancy (Nettle, Coall, & Dickins, 2011). Experiencing a more predictable adolescent environment indirectly predicts more restricted sociosexual behaviors and greater contraceptive use in early adulthood (Brumbach, Figueredo, & Ellis, 2009). Simpson and his colleagues (2012) directly pitted predictability levels during the first years of life against predictability levels at middle-childhood and adolescence and found that only the former uniquely forecasted fewer sexual partners by age 23. These findings also suggest that early-life predictability may exert unique effects on life history outcomes, above and beyond the impact of environmental harshness.

Parental Support and Attachment as Mediators

The information contained in early local environments must be detected by the growing child's developmental system to guide his or her subsequent development, but young children are typically not fully aware of the conditions that characterize their local environment. Parents, therefore, function as mediating agents, providing their children with information about the local environment primarily through the quality of their parenting (Belsky et al., 1991). Indeed, the quality and reliability of parental care varies considerably depending on the local environment (e.g., Conger, Cui, Bryant, & Elder, 2002; McLoyd, 1990, 1998; Quinlan, 2007), with most parents finding it more difficult to provide high-quality, supportive care in stressful conditions (Belsky & Jaffee, 2006; Crnic & Low, 2002). The quality of parental care, therefore, should be a highly valid cue indexing conditions in the local environment (Del Giudice & Belsky, 2011; Simpson, 1999).

A LHT perspective contends that harsh and/or unpredictable early-life environments should suppress the quality of parental care that children receive, leading to the development of faster reproductive strategies (more unrestricted sociosexuality; Belsky et al., 1991; Chisholm, 1993; Ellis, 2004). This hypothesis has garnered some support in a few prospective longitudinal studies that have examined how girls' sexual development is impacted by different types of parental disturbances, including father absence (Ellis & Essex, 2007), maternal separation and lack of paternal involvement (Nettle et al., 2011), and maternal depression (Belsky et al., 2012). Parental disruption has also been linked to lower-quality romantic relationships (Conger et al.,

2000; Cui & Fincham, 2010). Hence, this evidence also indicates that the quality of parental care might be a primary mechanism through which early environmental conditions mold reproductive strategies.

However, we still do not know *how* early parental care shapes the development of reproductive strategies into adulthood. One likely possibility is that the quality or reliability of early parental care creates beliefs and expectations in children regarding their future interactions in the wider world, which then direct their later psychological and behavioral adjustment (Del Giudice, 2009; Simpson & Belsky, 2008). This process is likely regulated by the attachment system, a species-typical, innate psychobiological system that motivates individuals to seek proximity to supportive others (attachment figures), especially in stressful conditions (Bowlby, 1969/1982). When a threat is detected, the attachment system launches a cascade of behavioral, psychological, and physiological responses designed to elicit support from caregivers to help restore feelings of physical and/or emotional safety. Early caregiving experiences also shape beliefs and expectations about the availability of supportive others in times of need, providing valuable information about the safety and predictability of the environment in which a child lives. Caregivers who provide good, reliable support instill positive expectations about the availability of supportive others (secure attachment representations), whereas those who provide inconsistent or poor support instill negative expectations regarding availability (insecure attachment representations). Once formed, attachment representations influence an individual's close relationships throughout his or her life (Bowlby, 1969/1982).

A great deal of research has also revealed that securely attached individuals prefer long-term relationships and function better in them (see Mikulincer & Shaver, 2016). For example, individuals who are securely attached in infancy display better conflict resolution skills and more positive emotions in their adult romantic relationships (Simpson, Collins, Tran, & Haydon, 2007), and they are rated as having higher-quality romantic relationships (Roisman, Collins, Sroufe, & Egeland, 2005). Moreover, inducing attachment security experimentally with priming techniques increases the desire for long-term relationships (Gillath & Schachner, 2006), and cross-sectional studies have shown that securely attached adults are more committed and supportive in their romantic relationships (e.g., Collins & Feeney, 2000; Simpson, 1990), whereas avoidantly attached adults (who represent one of two primary types of attachment insecurity) prefer short-term relationships and become less emotionally involved when in longer-term ones (Birnbaum, 2010; Schachner & Shaver, 2004).

Viewed as a whole, these findings imply that attachment representations ought to mediate the relation between exposure to predictable versus unpredictable early environments and reproductive strategies (Del Giudice, 2009; Simpson & Belsky, 2008). More specifically, exposure to

more predictable early-life environments should facilitate more reliable, higher-quality parental care, which in turn should instill secure attachment representations, eventually resulting in longer-term mating preferences and slower (more restricted) sociosexual orientations.

The MLSRA Study and Findings

To test these ideas prospectively and longitudinally, we (Szepsenwol et al., in press) analyzed data collected as part of the MLSRA (Sroufe et al., 2005). The MLSRA has followed approximately 180 individuals from before they were born into middle adulthood. All of the participants were born in the mid-1970s to first-time mothers, all of whom were living below the poverty line at the time of birth. At multiple points of development across the lifespan, the MLSRA has excellent measures of each participant's early-life environment (e.g., coder-rated measures of the predictability and harshness of each environment), coder-rated observational measures of parenting quality/support based on videotaped mother/child interactions early in life, and interview measures (coded by observers) of attachment representations and markers of restricted (slow) versus unrestricted (fast) sociosexuality from late adolescence and early adulthood.

Measures

What makes this study unique is the nature and quality of the measures, particularly those relevant to certain components and stages of the Belsky et al. (1991) model (see Figure 1.1). *Early predictability* was assessed by three items from the Life Events Schedule (LES; Egeland, Breitenbucher, & Rosenberg, 1982). These interview-based items asked each mother to report and discuss the disruptive nature of three types of changes in her life during the preceding year: (a) changes in employment status (e.g., periods of unemployment), (b) changes in residence (e.g., moving to a different house or apartment), and (c) changes in cohabitation status (e.g., whether and how often romantic partners moved in or out of the house/apartment). Each item was then rated by coders for the degree of disruption associated with each event on a scale of 0 (*no disruption*) to 3 (*severe disruption*). This measure encompassed the first four years of each participant's life when the LES was administered (when he or she was 12, 18, and 48 months old). Following prior studies (e.g., Simpson et al., 2012; Szepsenwol et al., 2015), we first created an accumulated unpredictability measure by summing the three items from all three assessments. We then subtracted this score from the maximum possible score to create an accumulated predictability score, which was then divided by three to form a 0 (*highly unpredictable*) to 9 (*highly predictable*) scale.

Early harshness was indexed by socioeconomic status (SES) during the first years of life for each participant. SES is a common harshness indicator in Western societies, as it is linearly related to most sources of morbidity and mortality (Adler, Boyce, Chesney, Folkman, & Syme, 1993; Chen, Matthews, & Boyce, 2002). The first SES assessment (at 42 months) was based on mothers' educational attainment and the revised version of the Duncan Socioeconomic Index (SEI; Duncan, 1961; Stevens & Featherman, 1981). The second assessment (at 54 months) was based on just mothers' SEI. SES scores were transformed to *t* scores within each assessment period to remove negative values, and the average of the 42- and 54-month scores served as our measure of early harshness.

Early maternal support was assessed by videotaped social interactions between each mother and her child (participant). When participants were 24 and 42 months old, they and their mothers were observed completing problem-solving and teaching tasks. These tasks gradually increased in complexity until they became too difficult for each child to solve on his or her own. Mothers were instructed to first allow their child to attempt the task independently, and then to step in and offer help if/when they thought it was appropriate. Each videotaped session was rated by coders for mothers' supportive presence on 7-point scales. High scores were given to mothers who showed interest and were attentive to the needs of their child, responded contingently to their child's emotional signals, and reinforced their child's success. Low scores were given to mothers who were distant, hostile, and/or unsupportive. The average of the 24- and 42-month scores was our measure of early maternal support.

Attachment representations were assessed by the Adult Attachment Interview (AAI; George, Kaplan, & Main, 1985) when participants were 19 years old. The AAI is a well-validated, semi-structured interview that assesses the degree to which individuals have a coherent narrative about their early experiences with caregivers (parents), primarily between the ages of 5 and 12. Participants were asked to describe their early relationships with their caregivers and to discuss periods of separation, rejection, abuse, and loss. The transcribed AAIs were then rated by coders on 9-point scales using Main and Goldwyn's (1998) coding system. We treated the *coherence of mind* scale, which assesses each individual's ability to freely explore his or her feelings about childhood experiences in an organized/emotionally well-regulated versus a non-organized/emotionally dysregulated manner, as our measure of attachment security. The coherence of mind scale is routinely used for this purpose (e.g., Raby, Cicchetti, Carlson, Egeland, & Collins, 2013; Roisman, Madsen, Hennighausen, Sroufe, & Collins, 2001).

Sociosexuality in early adulthood was assessed from an interview that participants completed when they were 23 years old. More specifically, the coding of sociosexuality was based on participants' responses to 14 interview

items that asked about their current romantic relationship, their relationship history within the past two years, and their ideal relationship. Two coders rated participants' responses to all 14 items for evidence of restricted versus unrestricted sociosexuality on a 5-point scale. A rating of 5 was given to participants who displayed no evidence of short-term dating or sexual promiscuity, who wanted to be in a romantic relationship with one person, and/or who were in a long-term romantic relationship (or had been in one recently). A rating of 1 was given to participants who reported multiple dating and sexual partners (most or all of which were short term), and who were interested in dating multiple people. The average rating of the two coders served as our measure of sociosexuality in early adulthood.

In addition, we assessed the *current predictability* of each participant's environment during the 23-year assessment. Current predictability was measured by the same three items used to assess early predictability (i.e., changes in employment status, changes in residence, and changes in cohabitation status during the past year). Coders rated each interview-based item for level of disruption on a scale from 0 (*no disruption*) to 3 (*severe disruption*). The current predictability measure was then computed by summing the ratings and subtracting the sum from the maximum possible sum to create a 0 (*highly unpredictable*) to 9 (*highly predictable*) scale. We used this measure in part to determine whether the effects of early-life predictability remained significant when current predictability was statistically controlled.

Results

To determine whether early predictability uniquely (independently) predicted greater restricted sociosexuality at age 23, we conducted hierarchical regression analyses. Consistent with our main hypothesis, greater early-life predictability forecasted more restricted sociosexuality at age 23. Current predictability also uniquely predicted greater restricted sociosexuality but just incrementally (i.e., the effects of early predictability still remained significant). Not surprisingly, gender was also a unique predictor, revealing that men were more unrestricted than women. Gender, however, did *not* moderate any of the effects of early or current predictability on sociosexuality in early adulthood.

We next tested whether early-life supportive parenting (based on behavioral observations of maternal supportive presence when participants were 2.5 and 3.5 years old) and secure attachment representations in adolescence (based on AAI coherence of mind scores at age 19) serially mediated the connection between exposure to predictability early in life and restricted sociosexuality at age 23. We used structural equation modeling (SEM) to accomplish this. The general path model we tested is shown in Figure 1.2. Consistent with our mediation hypothesis, exposure to more predictable
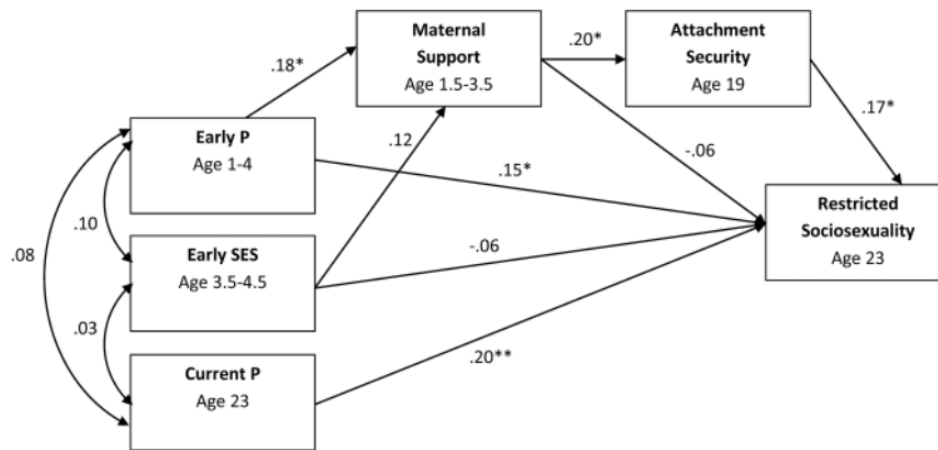
Figure 1.2   Mediation analysis: Direct and indirect effects of early predictability (P) on restricted sociosexuality in early adulthood. Effects are estimated using full information maximum likelihood (FIML). N = 155. (Szepsenwol et al., in press). Reprinted with permission from the American Psychological Association. * p < .05 ** p < .01

environments early in life was related to more supportive parenting from participants' mothers during the same time period, above and beyond the effects of early harshness. In addition, higher-quality early maternal support predicted more secure attachment representations at age 19, which in turn predicted more restricted sociosexuality at age 23.

It is important to note that the indirect effect shown in Figure 1.2 explained only 4% of the total effect of early predictability on adult sociosexuality. Additionally, the direct effect of early predictability on restricted sociosexuality in adulthood remained significant, as did the effect of current predictability. Finally, early maternal support did *not* directly predict restricted sociosexuality at age 23 (see Figure 1.2). In sum, these findings indicate that the effect of early predictability on restricted sociosexuality in early adulthood is partially mediated by early supportive parenting through attachment security in late adolescence. These findings provide new, prospective longitudinal support for several key components of Belsky et al.'s (1991) evolutionary model of social development.

TRAIT CLUSTERS ASSOCIATED WITH RESTRICTED (SLOW) AND UNRESTRICTED (FAST) SOCIOSEXUALITY

To this point, we have mainly speculated about the purported evolutionary functions of certain personality traits and stable individual differences. An evolutionary approach suggests that certain traits ought to cluster together to facilitate the successful enactment of certain reproductive strategies, resulting in specific personality profiles. However, to the extent that

different mating strategies were differentially successful in different types of early environments during evolutionary history, individuals should have adopted a strategy that was, on average, the most successful in response to the specific demands of their environment.

Reproduction, of course, involves much more than simply mating. It also involves courtship rituals, intersexual competition to attract and retain mates, and often considerable parenting following the conception of children. For this reason, mating strategies should involve clusters of different personality characteristics relevant to different aspects of successful reproduction (e.g., attracting a mate, competing with same-sex competitors, parenting children). Recall the earlier example of John, who is extraverted, an uninhibited risk-taker, and sexually unrestricted. These specific traits may cohere because they support a short-term, opportunistic, fast mating strategy in which emotional ties with partners are weaker and more transient (i.e., fast or *unrestricted* or strategy; see Griskevicius et al., 2013; Simpson & Gangestad, 1991a). With respect to trade-offs, this mating strategy entails earlier over delayed reproduction and offspring quantity over offspring quality. To enact a fast (unrestricted) mating strategy successfully, a person must be willing to enter new situations and novel environments in order to meet prospective mates and attempt to captivate their interest. Consequently, individuals who adopt a fast (unrestricted) mating strategy must continually be motivated to approach the potential rewards that might be found in novel situations and involve changing opportunities, including mating opportunities. They cannot be inhibited, afraid, or constrained because such tendencies would hinder or derail interactions with new potential partners. Unrestricted individuals, in other words, cannot be risk-averse or overly concerned about making mistakes that occasionally result in bad outcomes. During evolutionary history, therefore, these personality trait clusters should have facilitated the enactment of fast (unrestricted) mating strategies in response to these environments.

A very different personality profile is needed to successfully enact a restricted (slow) mating strategy. A restricted strategy is centered on long-term commitments in which emotional ties with partners are strong and enduring (Simpson & Gangestad, 1991a). This strategy involves making trade-offs that favor delayed over earlier reproduction and offspring quality over offspring quantity. Individuals who enact a slow (restricted) mating strategy are not easily drawn away from their current partners and relationships by the prospect of other attractive alternative partners. Instead, they remain committed to the partners and relationships in which they have already invested, assuming their current partner is sufficiently satisfactory. This explains why lower extraversion and higher constraint tends to facilitate the enactment of restricted mating strategies.

To study these trait clusters, Gangestad and Simpson (1990; Simpson & Gangestad, 1991b) investigated how scores on the Sociosexual Orientation Inventory (SOI; Simpson & Gangestad, 1991a) correlate with trait scales from Tellegen's (1982) Multidimensional Personality Questionnaire (MPQ) in young, single adults. The MPQ contains scales that assess various personality traits, including the Big Five. Higher scores on the SOI (i.e., having a faster, short-term, unrestricted mating orientation) loaded on two higher-order factors: *Extraversion* (SOI factor loading = .39) and *Lack of constraint* (SOI loading = .47). In particular, individuals who have a faster (more unrestricted) mating strategy are more extraverted/socially potent as well as less constrained/inhibited, less harm-avoidant, and poorer at self-regulation. Those who have a slower (more restricted) mating strategy, on the other hand, are more introverted, constrained, more harm-avoidant, and possess better self-regulation skills. These findings are consistent with prior research by Eysenck (1976), who found similar patterns of associations between sexual attitudes/behaviors and personality traits. They are also consistent with additional work linking sociosexual orientations with similar personality traits (e.g., T. M. Wright & Reise, 1997).

This leads us back to the examples of John and Tim. Why, from an evolutionary perspective, do these two individuals have the specific trait profiles they do? The answer may be that their clusters of traits are the ones that are best suited for John and Tim to compete for and attract mates, to successfully interact with other people, and perhaps even to parent, given their developmental histories. According to both the evolutionary model of social development (Belsky et al., 1991) and our recent findings (Szepsenwol et al., in press), John was probably raised in a stressful, unpredictable home environment by parents who had an unstable relationship and did not invest much time or effort in parenting him. He most likely learned from an early age that he had to be self-sufficient, had to compete with others and take risks in order to get attention and "get ahead" in life, and could not become too close to others without feeling vulnerable or being taken advantage of. John's early experiences, therefore, shunted him down a fast (unrestricted) pathway, and the specific profile of personality traits that he developed facilitates the successful enactment of his mating strategy.

Tim, in contrast, was most likely raised in a less stressful, more predictable home environment by parents who had a stable relationship and invested more time and effort in parenting and supporting him. He probably learned early on that he could count on other people to help and support him, he could "get ahead" in life by working cooperatively with others in the context of emotionally close, long-term relationships, and it was actually beneficial to get close to others and work collaboratively with them, especially during difficult times. Tim's early experiences, in other words, led

him down a slow (restricted) pathway, and the trait profile he developed promotes the successful enactment of his mating strategy.

ALTERNATIVE EVOLUTIONARY MODELS AND THE ROLE OF CULTURE

As mentioned earlier, a life history perspective is just one of several evolutionary-based approaches that can account for the variability that exists in personality and associated mating strategies (Buss, 2009). Such variation may also be created and maintained by costly signaling processes, environmental heterogeneity in fitness optima, frequency-dependent selection, and/or ecologically contingent changes in how individuals behave when exposed to different types of environments. Many of these processes operate within the context of trade-off decisions that individuals make, either consciously or unconsciously, as they navigate through their lives.

Costly signaling models (McAndrew, 2002; Miller, 2007) propose that individual differences emerge when people differ in their ability to engage in certain acts that "honestly" signal their status, skills, or socially valued traits to other people. Individuals who have abundant resources and want to impress others, for example, are in a better position to be altruistic and generous compared to those who have few or no resources, even if they are strongly motivated to impress other people.

Environmental heterogeneity in fitness optima models (e.g., Chen, Burton, Greenberger, & Dmitrieva, 1999; Penke et al., 2007) suggest that individual differences exist when selection pressures favor different (multiple) levels of a personality trait in different environments. Greater risk-taking, for instance, may yield more positive fitness outcomes (e.g., greater reproductive success) in environments where risks have greater payoffs, but being more cautious is likely to be associated with better fitness returns in environments where risks often result in injuries or premature death.

Frequency-dependent selection models (e.g., Gangestad & Simpson, 1990; Nettle, 2006) posit that individual differences appear and are maintained depending on the relative frequency of individuals who display different kinds or levels of traits within a population. A classic example is the relative prevalence of "cheaters" (such as psychopaths) versus non-cheaters in a population. When cheaters are comparatively few in number, these individuals can often exploit the cooperative inclination of the vast majority of people who cooperate and behave honestly and fairly with others. The success of a cheating strategy rapidly diminishes, however, as increasing numbers of people become cheaters (Mealey, 1995).

Finally, individual differences may result from the tendency for people to alter how they behave when in different or changing environments

(e.g., Belsky, 1999; Gangestad & Simpson, 2000). These ecological-contingent models claim that individuals have evolved cognitive adaptations that motivate them to shift their behavior in fitness-enhancing ways, depending on features of the current environment. For example, individuals who might normally pursue a fast mating strategy in most environments should facultatively shift and enact a slower mating strategy if their mate value declines, mate options become poor or limited, or the environment suddenly demands biparental care in order for offspring to survive and thrive (see Gangestad & Simpson, 2000). To reiterate, many of these evolutionary-based processes operate as individuals make many important trade-off decisions across their lives. Consequently, LHT functions as a metatheory that connects and integrates many of these "individual difference-generating" evolutionary processes.

Where do culture and cultural differences fit within life history thinking? Life history models typically assume that high levels of harshness and unpredictability should have similar effects on people who live in different cultures. Most models, however, are flexible enough to allow for cultural differences to impact the circumstances under which high levels of harshness or unpredictability influence life history outcomes. Cultural norms, rules, expectations, or practices, for example, are likely to affect which specific forms of harshness or unpredictability tend to be particularly distressing. Extreme levels of unpredictability due to instability or turmoil within families, for instance, may be especially upsetting to people who live in highly interdependent cultures, where stable, harmonious family relations are strongly valued. On the flipside, high levels of harshness associated with chronic lack of resources (e.g., insufficient money) may be particularly upsetting to people who live in highly independent cultures, where being self-sufficient, autonomous, and "one's own person" are paramount virtues.

Cultural differences might also influence the way in which people react to and deal with high, sustained levels of harshness or unpredictability. For example, people who live in highly interdependent cultures that value tightly connected social networks anchored by close, longstanding interpersonal relationships may weather periods of harshness or unpredictability better than those who live in highly independent, more socially fragmented cultures. One possible reason for this is that people who reside in highly interdependent cultures tend to have well-established social connections and social structures that may allow them to work together more effectively when they face adverse conditions, whereas those who live in highly independent cultures are less likely to have—and may find it more difficult to build and maintain—these supportive social networks, particularly during stressful times. These ideas are speculative, but they suggest how cultural differences could be more fully integrated into life history models and thinking.

CONCLUSION

In conclusion, evolutionary theories, models, and principles have a great deal to offer personality psychology. In this chapter, we have highlighted how certain evolutionary theories—especially those related to the framework of LHT—can generate novel, important insights into not only why certain personality traits exist but also how and why people vary on certain traits and why certain traits may cluster together. Evolutionary theories are able to provide unique insights in part because they ask and attempt to answer deeper "why" questions that center on the ultimate origins, purposes, and functions of specific traits and behaviors. The broader field of personality is now poised to take greater advantage of one of the most powerful sets of ideas in the social and life sciences—the modern evolutionary perspective. We hope that this chapter will help facilitate that process.

REFERENCES

Adler, N. E., Boyce, W. T., Chesney, M. A., Folkman, S., & Syme, S. L. (1993). Socio-economic inequalities in health: No easy solution. *Journal of the American Medical Association, 269*, 3140–3145.

Alcock, J., & Crawford, C. (2008). Evolutionary questions for evolutionary psychologists. In C. Crawford & D. Krebs (Eds.), *Foundations of evolutionary psychology* (pp. 25–46). New York, NY: Taylor & Francis.

Belsky, J. (1997). Attachment, mating, and parenting: An evolutionary interpretation. *Human Nature, 8*, 361–381.

Belsky, J. (1999). Modern evolutionary theory and patterns of attachment. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (pp. 141–161). New York, NY: Guilford.

Belsky, J., & Jaffee, S. (2006). The multiple determinants of parenting. In D. Cicchetti & D. Cohen (Eds.), *Developmental psychopathology: Vol. 3. Risk, disorder and adaptation* (2nd ed., pp. 38–85). New York, NY: Wiley.

Belsky, J., Schlomer, G. L., & Ellis, B. J. (2012). Beyond cumulative risk: Distinguishing harshness and unpredictability as determinants of parenting and early life history strategy. *Developmental Psychology, 48*, 662–673.

Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development, 62*, 647–670.

Birnbaum, G. E. (2010). Bound to interact: The divergent goals and complex interplay of attachment and sex within romantic relationships. *Journal of Social and Personal Relationships, 27*, 245–252.

Bouchard, T. J., Jr. (2004). Genetic influence of human psychological traits. *Current Directions in Psychological Science, 13*, 148–151.

Bowlby, J. (1969/1982). *Attachment and loss: Vol. 1. Attachment* (2nd ed.). New York, NY: Basic Books.

Brumbach, B. H., Figueredo, A. J., & Ellis, B. J. (2009). Effects of harsh and unpredictable environments in adolescence on development of life history strategies: A longitudinal test of an evolutionary model. *Human Nature, 20*, 25–51.

Buss, D. M. (2009). How can evolutionary psychology successfully explain personality and individual differences? *Perspectives on Psychological Science, 4*, 359–366.

Buss, D. M. (Ed.). (2016). *The handbook of evolutionary psychology* (2nd ed.). New York, NY: Wiley.

Charnov, E. L. (1993). *Life history invariants*. Oxford, UK: Oxford University Press.

Chen, C., Burton, M., Greenberger, E., & Dmitrieva, J. (1999). Population migration and the variation of dopamine D4 receptor (DRD4) allele frequencies around the globe. *Evolution and Human Behavior, 20*, 309–324.

Chen, E., Matthews, K. A., & Boyce, W. T. (2002). Socioeconomic differences in children's health: How and why do these relationships change with age? *Psychological Bulletin, 128*, 295–329.

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

Chisholm, J. S. (1996). The evolutionary ecology of attachment organization. *Human Nature, 7*, 1–38.

Chisholm, J. S. (1999). *Death, hope, and sex*. New York, NY: Cambridge University Press.

Collins, N. L., & Feeney, B. C. (2000). A safe haven: An attachment theory perspective on support seeking and caregiving in intimate relationships. *Journal of Personality and Social Psychology, 78*, 1053–1073.

Conger, R. D., Cui, M., Bryant, C. M., & Elder, G. H. (2000). Competence in early adult romantic relationships: A developmental perspective on family influences. *Journal of Personality and Social Psychology, 79*, 224–237.

Conger, R. D., Wallace, L. E., Sun, Y., Simons, R. L., McLoyd, V. C., & Brody, G. H. (2002). Economic pressure in African American families: A replication and extension of the family stress model. *Developmental Psychology, 38*, 179–193.

Crnic, K., & Low, C. (2002). Everyday stresses and parenting. In M. H. Bornstein (Ed.), *Handbook of parenting: Vol. 5. Practical issues in parenting* (2nd ed., pp. 243–267). Mahwah, NJ: Erlbaum.

Cui, M., & Fincham, F. D. (2010). The differential effects of parental divorce and marital conflict on young adult romantic relationships. *Personal Relationships, 17*, 331–343.

Darwin, C. (1859). *On the origins of species*. London, England: John Murray.

Darwin, C. (1981). *The descent of man, and selection in relation to sex.* Princeton, NJ: Princeton University Press. (Original work published 1871.)

Del Giudice, M. (2009). Sex, attachment, and the development of reproductive strategies. *Behavioral and Brain Sciences, 32*, 1–67.

Del Giudice, M., & Belsky, J. (2011). The development of life history strategies: Toward a multi-stage theory. In D. M. Buss & P. H. Hawley (Eds.), *The evolution of personality and individual differences* (pp. 154–176). New York, NY: Oxford University Press.

Del Giudice, M., Gangestad, S. W., & Kaplan, H. S. (2016). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (2nd ed., pp. 88–114). New York, NY: Wiley.

Donaldson-Matasci, M. C., Lachmann, M., & Bergstrom, C. T. (2008). Phenotypic diversity as an adaptation to environmental uncertainty. *Evolutionary Ecology Research, 10*, 493–515.

Draper, P., & Harpending, H. (1982). Father absence and reproductive strategy: An evolutionary perspective. *Journal of Anthropological Research, 38*, 255–273.

Duncan, O. (1961). A socioeconomic index for all occupations. In A. J. Reiss, Jr. (Ed.), *Occupations and social status* (pp. 109–138). New York, NY: Free Press.

Eastwick, P. W. (2009). Beyond the Pleistocene: Using phylogeny and constraint to inform the evolutionary psychology of human mating. *Psychological Bulletin, 135*, 794–821.

Egeland, B. R., Breitenbucher, M., & Rosenberg, D. (1982). Prospective study of the significance of life stress in the etiology of child abuse. *Journal of Consulting and Clinical Psychology, 48*, 195–205.

Ellis, B. J. (2004). Timing of pubertal maturation in girls. *Psychological Bulletin, 130*, 920–958.

Ellis, B. J., Del Giudice, M., Dishion, T. J., Figueredo, A. J., Gray, P., Griskevicius, V., . . . Wilson, D. S. (2012). The evolutionary basis of risky adolescent behavior: Implications for science, policy, and practice. *Developmental Psychology, 48*, 598–623. doi: 10.1037/a0026220

Ellis, B. J., & Essex, M. J. (2007). Family environments, adrenarche, and sexual maturation: A longitudinal test of a life history model. *Child Development, 78*, 1799–1817.

Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). Fundamental dimensions of environmental risk: The impact of harsh versus unpredictable environments on the evolution and development of life history strategies. *Human Nature, 20*, 204–268.

Eysenck, H. J. (1976). *Sex and personality*. London, England: Open Books.

Fraley, R. C., Brumbaugh, C. C., & Marks, M. J. (2005). The evolution and function of adult attachment: A comparative and phylogenetic analysis. *Journal of Personality and Social Psychology, 89*, 731–746.

Gangestad, S. W., & Simpson, J. A. (1990). Toward an evolutionary history of female sociosexual variation. *Journal of Personality, 58*, 69–96.

Gangestad, S. W., & Simpson, J. A. (2000). Trade-offs, the allocation of reproductive effort, and the evolutionary psychology of human mating. *Behavioral and Brain Sciences, 23*, 624–644.

George, C., Kaplan, N., & Main, M. (1985). *The adult attachment interview*. Unpublished protocol, Department of Psychology, University of California, Berkeley.

Gillath, O., & Schachner, D. A. (2006). How do sexuality and attachment interrelate? Goals, motives, and strategies. In M. Mikulincer & G. S. Goodman (Eds.), *Dynamics of romantic love: Attachment, caregiving, and sex* (pp. 337–355). New York, NY: Guilford Press.

Griskevicius, V., Ackerman, J. M., Cantú, S. M., Delton, A. W., Robertson, T. E., Simpson, J. A., . . . Tybur, J. M. (2013). When the economy falters do people spend or save? Responses to resource scarcity depend on childhood environments. *Psychological Science, 24*, 197–205.

Hinde, R. A. (1986). Some implications of evolutionary theory and comparative data for the study of human prosocial and aggressive behaviour. In D. Olweus, J. Block, & M. Radke-Yarrow (Eds.), *Development of anti-social and prosocial behaviour* (pp. 13–32). Orlando, FL: Academic Press.

Horn, H., & Rubenstein, D. (1984). Behavioral adaptations and life history. In J. Krebs & N. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (2nd ed., pp. 279–300). Oxford, England: Blackwell.

Kaplan, H. S., & Gangestad, S. W. (2005). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 68–95). New York, NY: Wiley.

Kenrick, D. T., Griskevicius, V., Neuberg, S. L., & Schaller, M. (2010). Renovating the pyramid of needs: Contemporary extensions built upon ancient foundations. *Perspectives in Psychological Science, 5,* 292–314.

Kotchick, B. A., Shaffer, A., Forehand, R., & Miller, K. S. (2001). Adolescent sexual risk behavior: A multi-system perspective. *Clinical Psychology Review, 21,* 493–519.

Low, B. S., Hazel, A., Parker, N., & Welch, K. B. (2008). Influences on women's reproductive lives: Unexpected ecological underpinnings. *Cross-Cultural Research, 42,* 201–219.

MacDonald, K. B. (1995). Evolution, the five-factor model, and levels of personality. *Journal of Personality, 63,* 525–567.

Main, M., & Goldwyn, R. (1998). *Adult attachment rating and classification systems* (Version 6). Unpublished manuscript, University of California, Berkeley.

McAndrew, F. T. (2002). New evolutionary perspectives on altruism: Multilevel selection and costly signaling theories. *Current Directions in Psychological Science, 11,* 79–82.

McLoyd, V. C. (1990). The impact of economic hardship on black families and children: Psychological distress, parenting, and socioemotional development. *Child Development, 61,* 311–346.

McLoyd, V. C. (1998). Socioeconomic disadvantage and child development. *American Psychologist, 53,* 185–204.

Mealey, L. (1995). The sociobiology of sociopathy: An integrated evolutionary model. *Behavioral and Brain Sciences, 18,* 523–599.

Mikulincer, M., & Shaver, P. R. (2016). *Attachment in adulthood: Structure, dynamics, and change* (2nd ed.). New York, NY: Guilford Press.

Miller, G. (2007). Sexual selection for moral virtues. *Quarterly Review of Biology, 82,* 97–125.

Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist, 61,* 622–631.

Nettle, D., Coall, D. A., & Dickins, T. E. (2011). Early-life conditions and age at first pregnancy in British women. *Proceedings of the Royal Society B, 278,* 1721–1727.

Penke, L., Denissen, J. J., & Miller, G. F. (2007). The evolutionary genetics of personality. *European Journal of Personality, 21,* 549–587.

Pinker, S. (1994). *The language instinct.* New York, NY: William Morrow.

Promislow, D., & Harvey, P. (1990). Living fast and dying young: A comparative analysis of life-history variation among mammals. *Journal of the Zoological Society of London, 220,* 417–437.

Quinlan, R. J. (2007). Human parental effort and environmental risk. *Proceedings of the Royal Society B, 274,* 121–125.

Raby, K. L., Cicchetti, D., Carlson, E. A., Egeland, B., & Collins, A. W. (2013). Genetic contributions to continuity and change in attachment security: A prospective, longitudinal investigation from infancy to young adulthood. *Journal of Child Psychology and Psychiatry, 54,* 1223–1230.

Roisman, G. I., Collins, W. A., Sroufe, L. A., & Egeland, B. (2005). Predictors of young adults' representations of and behavior in their current romantic relationship:

Prospective tests of the prototype hypothesis. *Attachment and Human Development, 7,* 105–121.

Roisman, G. I., Madsen, S. D., Hennighausen, K. H., Sroufe, L. A., & Collins, W. A. (2001). The coherence of dyadic behavior across parent-child and romantic relationships as mediated by the internalized representation of experience. *Attachment and Human Development, 3,* 156–172.

Schachner, D. A., & Shaver, P. R. (2004). Attachment dimensions and sexual motives. *Personal Relationships, 11,* 179–195.

Simpson, J. A. (1990). Influence of attachment styles on romantic relationships. *Journal of Personality and Social Psychology, 59,* 971–980.

Simpson, J. A. (1999). Attachment theory in modern evolutionary perspective. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (pp. 115–140). New York, NY: Guilford Press.

Simpson, J. A., & Belsky, J. (2008). Attachment theory within a modern evolutionary framework. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (2nd ed., pp. 131–157). New York, NY: Guilford Press.

Simpson, J. A., & Belsky, J. (2016). Attachment theory within a modern evolutionary framework. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (3rd ed., pp. 91–116). New York, NY: Guilford Press.

Simpson, J. A., & Campbell, L. (2016). Methods of evolutionary sciences. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (2nd ed., pp. 115–135). New York, NY: Wiley.

Simpson, J. A., Collins, W. A., Tran, S., & Haydon, K. C. (2007). Attachment and the experience and expression of emotions in romantic relationships: A developmental perspective. *Journal of Personality and Social Psychology, 92,* 355–367.

Simpson, J. A., & Gangestad, S. W. (1991a). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology, 60,* 870–883.

Simpson, J. A., & Gangestad, S. W. (1991b). Personality and sexuality: Empirical relations and an integrative theoretical model. In K. McKinney & S. Sprecher (Eds.), *Sexuality in close relationships* (pp. 71–92). Hillsdale, NJ: Erlbaum.

Simpson, J. A., & Gangestad, S. W. (2001). Evolution and relationships: A call for integration. *Personal Relationships, 8,* 341–355.

Simpson, J. A., Griskevicius, V., Kuo, S. I. C., Sung, S., & Collins, W. A. (2012). Evolution, stress, and sensitive periods: The influence of unpredictability in early versus late childhood on sex and risky behavior. *Developmental Psychology, 48,* 674–686.

Sroufe, L. A., Egeland, B., Carlson, E. A., & Collins, W. A. (2005). *The development of the person: The Minnesota study of risk and adaptation from birth to adulthood.* New York, NY: Guilford Press.

Stevens, G., & Featherman, D. L. (1981). A revised socioeconomic index of occupational status. *Social Science Research, 10,* 364–395.

Szepsenwol, O., Griskevicius, V., Simpson, J. A., Young, E. S., Fleck, C., & Jones, R. E. (in press). The effect of predictable early childhood environments on sociosexuality in early adulthood. *Evolutionary Behavior Sciences.*

Szepsenwol, O., Simpson, J. A., Griskevicius, V., & Raby, K. L. (2015). The effect of unpredictable early childhood environments on parenting in adulthood. *Journal of Personality and Social Psychology, 109*, 1045–1067.

Tellegen, A. (1982). *Brief manual for the Multidimensional Personality Questionnaire.* Unpublished manuscript, University of Minnesota, Minneapolis, MN.

Tinbergen, N. (1963). On the aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*, 410–433.

Tooby, J., & Cosmides, L. (1992). Psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 19–136). New York, NY: Oxford University Press.

Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., . . . Yamauchi, T. (2006). Growth rates and life histories in twenty-two small-scale societies. *American Journal of Human Biology, 18*, 295–311.

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution.* Oxford, England: Oxford University Press.

Wilson, M., & Daly, M. (2005). Carpe diem: Adaptation and devaluing the future. *Quarterly Review of Biology, 80*, 55–60.

Wright, R. (1994). *The moral animal.* New York, NY: Vintage.

Wright, T. M., & Reise, S. P. (1997). Personality and unrestricted sexual behavior: Correlations of sociosexuality in Caucasian and Asian college students. *Journal of Research in Personality, 31*, 166–192.