

The Development of Human Reproductive Strategies: Progress and Prospects

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Abstract

An evolutionary-biological perspective on the effects of the extrafamilial and familial environment on multiple psychological, behavioral, and even somatic features of children's development challenges prevailing thinking about human development, which regards some contextual conditions and their sequelae as "good" and others as "bad." Theory and research on the development of human reproductive strategies based on such evolutionary thinking has evolved substantially over the past two decades. In this article, I review two decades of theory and research findings pertaining to the development of reproductive strategies—highlighting the contextual regulation of pubertal timing, the distinctive role of fathers, individuals' differential susceptibility to rearing influences, mechanisms of influence, and new ways of conceptualizing influential environmental features—and outline future directions for research.

Keywords

parenting, socialization, evolution, puberty, sexual behavior, biology

Most research seeking to illuminate how environmental experiences influence human development, especially in the early years of life, is guided by a mental-health framework, which presumes that certain environmental influences and outcomes (e.g., sensitive parenting–secure attachment) are good and others (e.g., harsh parenting–aggression) are bad. A reproductive-strategy perspective, based on life-history theory—an evolutionary-biological approach to development—regards diverse developmental processes and products rather differently. What many conceptualize as manifestations of "nonoptimal" development (e.g., insecure attachment, aggression, risk taking, early sexual debut), evolutionary-minded thinkers regard as potential alternative tactics for dispersing genes across generations and thereby enhancing reproductive fitness under the ecological conditions that give rise to them. An evolutionary perspective is thus appreciative of the benefits, not just the costs, of putatively problematic functioning (Ellis & Bjorklund, 2012). Research on human development informed by life-history theory, launched some two decades ago, has made significant contributions to the field, though many issues merit additional attention.

In the Beginning

In a seminal paper that stimulated a somewhat-delayed cascade of theoretical developments and empirical studies on the role of childhood experience in shaping reproductive strategy, anthropologists Draper and Harpending (1982) argued that

girls growing up in father-present and father-absent homes develop different psychologies and behaviors in order to serve the same fitness goals. Girls whose fathers are absent develop sexually promiscuous behavior consistent with an expectation that paternal investment in childrearing will not be forthcoming and that pair bonds will not be enduring. In contrast, girls from father-present households develop as if anticipating the opposite, deferring sexual activity once they reach biological maturity and seeking to establish and maintain enduring and close intimate adult relationships.

What was unique to Draper and Harpending's (1982) argument was the casting of the influence of early experience in the family in evolutionary terms—emphasizing reproductive fitness, parental investment, pair bonds, and reproductive strategy (i.e., not mental health). But two things were missing from their analysis. First, no developmental process was offered to explain how the absence of fathers shapes individuals' functioning in adolescence and adulthood. Second, no original predictions were advanced, which raised the question of whether the reproductive-strategy perspective was anything more than old wine in a new bottle.

Consideration of these limitations led us (Belsky, Steinberg, & Draper, 1991) to advance an evolutionary theory

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of socialization linking childhood experience, interpersonal orientation, and reproductive strategy. This theory has come to be known as *psychosocial acceleration theory*, although it is expressly about the regulation—not just the acceleration—of development. Central to the theory, based as it was on more general life-history theory, is the thesis that stressful or supportive extrafamilial environments influence family dynamics, especially parent-child and marital/pair-bond relations. These then shape or regulate children's early emotional and behavioral development, including attachment security, and, thereby, subsequent social development, including sexual/mating behavior, pair bonding, and parenting styles. Following Draper and Harpending (1982), we (Belsky et al., 1991) argued that this complex and environmentally sensitive developmental system evolved as a means of fitting individuals to their anticipated future environments in order to enhance reproductive fitness (i.e., not mental health)—at least in the ancestral environments in which human development evolved.

Of central importance to psychosocial acceleration theory is the view that parent-child relationship processes (e.g., conflict, cooperation) and, in particular, attachment security/insecurity mediate the influence of stressors and supports external to the parent-child relationship on children's (a) general outlook on the world (trustful vs. mistrustful), (b) orientation toward others (opportunistic-exploitative vs. mutually beneficial), and (c) behavior. But what fundamentally distinguished this theory from all others addressing familial and extrafamilial influences on human development was its prediction regarding processes instantiating different rates of development.

Specifically, psychosocial acceleration theory posits that developmental experiences and psychological orientations regulate reproductive development by affecting the timing of puberty and, thereby, a cascade of processes involving sexual behavior, pair-bonding, and parenting style. Thus, accelerated development eventuating in a fast, quantity-oriented reproductive strategy is most likely to emerge in the context of a variety of stressors, including inadequate financial resources and parental marital discord, which would undermine parental well-being and thereby give rise to harsh, rejecting, insensitive, and/or inconsistent parenting; these factors would then foster in the child insecure attachment, a mistrustful view of the world, and an opportunistic-exploitative interpersonal orientation. Such developments would themselves stimulate earlier pubertal maturation and sexual debut, a tendency toward forming short-term and unstable pair bonds, and limited parental investment geared toward bearing more children but not caring for them intensively.

The alternative developmental trajectory, resulting in slower, quality-oriented reproductive and parenting strategies, would be induced by exposure to a supportive rearing environment characterized by spousal harmony and adequate financial resources. Such intrafamilial conditions, shaped by extrafamilial conditions, would give rise to sensitive, supportive, responsive, and affectionate parenting styles and, thereby, secure attachments, a trusting outlook, and a reciprocally

rewarding interpersonal orientation. Collectively, these developments would delay pubertal maturation and defer the onset of sexual activity, eventually fostering the formation of enduring pair bonds and greater parental investment in fewer offspring.

Testing the Puberty Prediction

In a thoughtful critique published alongside the original presentation of psychosocial acceleration theory, Maccoby (1991) argued that it fit males better than females. Just the opposite appears to be the case, however: Evidence has indicated that the general inability to predict pubertal timing in males is not just a function of measurement challenges (Belsky, Steinberg, et al., 2007; but see Ellis, Shirtcliff, Boyce, Dearnorff, & Essex, 2011), and new proposals have suggested that female reproductive strategies are more sensitive to familial and ecological conditions, whereas male strategies are more sensitive to peer experiences (Del Giudice, Ellis, & Shirtcliff, 2011; James, Ellis, Schlomer, & Garber, 2012). Therefore, in this article, I focus principally on female reproductive strategies, given the theory's distinguishing prediction regarding pubertal development. Male-specific extensions of the theory not focused on puberty, but grounded in sexual selection theory and emphasizing the influence of peers, have recently been advanced and subjected to empirical scrutiny (Del Giudice, 2009; Dishion, Ha, & Veronneau, 2012; James et al., 2012).

A comprehensive review of the evidence related to psychosocial acceleration theory's prediction regarding puberty led Ellis (2004, pp. 935–936) to conclude that “empirical research has provided reasonable, though incomplete” support for our original theorizing (Belsky et al., 1991). After noting that “there is converging evidence . . . that greater parent-child warmth and cohesion is [*sic*] associated with later pubertal development” in females, he went on to observe that “the proposed accelerating effect of parent-child conflict and coercion on pubertal development is yet to be clearly established.”

Subsequent research, including research by Ellis himself, has altered the evidentiary landscape. Ellis and Essex (2007) reported that in females, family nonsupportiveness during the preschool years—assessed using a composite index that included measures of authoritarian parenting and negative family relationships—was associated with advanced adrenarcheal status at age 7 and advanced maturation of secondary sex characteristics in fifth grade. Additional research showed that family disruption and, especially, father's social deviance—hypothesized to index problematic father-daughter relationships—predicted earlier age of menarche (Tither & Ellis, 2008). Relatedly, Costello, Sung, Worthman, and Angold (2007) discovered that maltreated girls reached pubertal maturity 8 months earlier than did nonmaltreated girls. We (Belsky, Steinberg, et al., 2007; Belsky, Steinberg, Houts, Halpern-Felsher, & The NICHD Early Child Care Research Network, 2010) extended this longitudinal work, showing not only that early maternal harshness predicted earlier menarche but that,

via this effect, it indirectly fostered greater sexual risk taking in adolescence. Finally, taking advantage of a natural experiment, Pesonen and her associates (2008) observed that young Helsinki girls who had been evacuated from their homeland during World War II and sent to live in Sweden and Denmark reached menarche at a younger age—and also bore more children by late adulthood—than did members of the same birth cohort who had remained at home, thereby avoiding the trauma of separation from their families.

Even if the effect of rearing on pubertal timing is noteworthy, it must be acknowledged that it is modest, such that observed accelerations of pubertal rates amount to differences in the range of 2 to 8 months (Ellis, 2004). Yet this does not preclude its functional importance vis-à-vis reproduction, as illustrated by Ellis's (2004, p. 936) insightful observation that "the time from menarche until 50% of (menstrual) cycles are ovulatory is approximately 1 year if menarche occurs before age 12 and 4.5 years if menarcheal age is 13 or older." Moreover, it remains conceivable that female pubertal timing was far more plastic before its dramatic decline over the past 150 years in the Western world and, consequently, that it was far more susceptible to the effects of rearing (Belsky et al., 1991).

Genetics, Gene-Environment Interaction, and Differential Susceptibility

The fact that pubertal timing is substantially heritable raises the possibility that the rearing effects under consideration are an artifact of genes shared by parents and daughters. Yet when Rowe (2000, p. 165) directly tested this proposition using a genetically informative design, he acknowledged that "the behavioral genetic view gave no knock-out punches." Moreover, although Mendle et al. (2006), using a children-of-twins design that controlled for maternal genetic inheritance, observed that effects of step-father presence on pubertal timing were most likely, even if not certainly, genetically mediated, Tither and Ellis (2008) drew just the opposite conclusion. These latter investigators relied on a sibling design that controlled for maternal genetic influences, paternal genetic influences, and family-based influences in their research on the influence of biological fathers' presence/absence on girls' age of menarche. Finally, Comings, Muhleman, Johnson, and MacMurray's (2002) finding documenting associations between an X-chromosome-linked androgen receptor GGC-repeat polymorphism and parental divorce, paternal absence, and earlier age of menarche could not be replicated by Jorm, Christensen, Rodgers, Jacomb, and Easteal (2004) using data from two epidemiological studies.

Rather than thinking in terms of genetic or environmental effects, it appears to be more productive to adopt the life-history view that there can be *alternative* and *conditional* reproductive strategies (Belsky, 2000), with the former more and the latter less susceptible to contextual regulation. Notably consistent with this perspective of differential susceptibility to environmental influences (Belsky, Bakermans-Kranenburg, &

van IJzendoorn, 2007) are results from two recent studies showing that both an estrogen-receptor gene (Manuck, Craig, Flory, Halder, & Ferrell, 2011) and physiological reactivity (Ellis et al., 2011) can be used to identify the degree to which females' pubertal development—and perhaps reproductive strategy generally—is regulated by rearing experiences.

The Distinctive Influence of the Father

Whereas we (Belsky et al., 1991) purposefully cast the net wider than father absence when it came to delineating environmental experiences and exposures that regulate the development of reproductive strategies—by highlighting the quality of parent-child and marital relations and extra-familial determinants of these—others embrace the original formulation of Draper and Harpending (1982) emphasizing fathers' influence: "Girls detect and internally encode information *specifically* about the quality of paternal investment . . . as a basis of calibrating . . . the timing of pubertal maturation and certain types of sexual behavior" (Ellis, 2004, p. 938, emphasis added).

Although some evidence has certainly implicated the influence of fathers on female pubertal development (e.g., Ellis & Essex, 2007) and risky sexual behavior (Ellis, Schlomer, Tilley, & Butler, 2012), we (Belsky, Steinberg, et al., 2007) failed to chronicle any paternal influence on pubertal development. What is ultimately needed are more studies like that of Ellis, McFadyen-Ketchum, Dodge, Pettit, and Bates (1999) examining the (unique) effects of one parent while discounting the effects of the other. Admittedly, research in this area is challenging because of the difficulty securing the involvement of or information about absent fathers and fathers whose parental investment is especially limited.

Conceptualizing the Environment

Psychosocial acceleration theory called attention to stressful and supportive rearing environments, arguing that under contextual conditions of risk and uncertainty, there is an inherit bio-logic to accelerated reproductive development. Although we (Belsky et al., 1991) appreciated that costs associated with accelerated development represented trade-offs geared toward reducing individuals' risk of dying before they reached reproductive age, it was Chisholm (1993) who called especial attention to local mortality rates. These, he argued, were what natural selection had shaped humans to monitor in order to more accurately forecast the future and regulate reproductive development. Evidence linking more dangerous rearing environments and shorter life expectancy with younger age of first birth are consistent with this claim (e.g., Geronimus, 1996; Griskevicius, Delton, Robertson, & Tybur, 2011; Johns, 2003; Nettle, Coall, & Dickins, 2011; Quinlan, 2010; Wilson & Daly, 1997). Still unknown, though, is whether these factors relate directly to pubertal timing or whether pubertal timing mediates these factors' effects on reproductive functioning.

Ellis, Figueredo, Brumbach, and Schlomer (2009) recently systematized the existing literature on life-history variation within and across species to highlight critically influential features of the environment. In so doing, they extended prevailing psychological models of how familial and extrafamilial stress and support (Belsky et al., 1991; Conger et al., 2002) and cumulative contextual risk (Sameroff, Seifer, Barocas, Zax, & Greenspan, 1987) shape human development. These evolutionary-minded developmentalists specifically called attention to extrinsic (or uncontrollable) morbidity-mortality rates (i.e., environmental harshness) and environmental unpredictability (i.e., the extent to which conditions fluctuate across individuals' life spans). Under harsh environmental conditions, individuals are at risk of dying before reaching reproductive age, which makes it bio-logical for them to develop faster, mature earlier, and initiate sexual activity sooner rather than later. Because predicting the future is particularly difficult under unpredictable environmental conditions, efforts to mitigate risk are less likely to pay off in terms of enhancing reproductive fitness than they might be in other circumstances. Parental investment should therefore be less intensive than it otherwise would be, thereby stimulating the faster development of offspring.

Although this new framework has yet to inform pubertal-timing research, recent longitudinal analyses have documented its utility in predicting faster life-history strategies in adolescence (Belsky, Schlomer, & Ellis, 2012) and young adulthood (Simpson, Griskevicius, Kuo, Sung, & Collins, 2012; see also Nettle et al., 2011). Future work should not only focus on pubertal timing but test this new formulation of critical environmental parameters that regulate reproductive strategies against more traditional strategies of conceptualizing influential features of the environment.

Additional consideration of the issue of environmental unpredictability led Frankenhuis and Panchanathan (2011) to offer a novel prediction regarding developmental plasticity and, thereby, the development of reproductive strategies: The time individuals take to "commit" to a particular developmental pathway should vary depending on the stability of evolutionarily informative cues. When contextual cues are stable, providing a seemingly reliable basis for predicting the future, developmental commitment to a conditional adaptive strategy should be made earlier rather than later in life; when such cues prove less reliable, however, the organism should maintain a more "open mind," deferring developmental commitment to one or another reproductive strategy. This view carries intriguing implications for the nature and timing of interventions aimed at preventing or remediating "problematic behavior" like sexual risk taking (Frankenhuis & Del Giudice, 2012).

Mechanisms of Influence

We (Belsky et al., 1991) called attention to the role that the child's attachment security played in conveying information about risk and uncertainty from the extrafamilial world

through the parent-child relationship to the child (Belsky, 1997; Chisholm, 1993). In light of extensive evidence that a variety of contextual stressors and supports influence parenting (Belsky & Jaffee, 2006) and that sensitive parenting causally influences attachment security (Bakermans-Kranenburg, van IJzendoorn, & Juffer, 2003), new evidence linking insecure infant-mother attachment at 15 months with early menarche (Belsky et al., 2010) is certainly noteworthy. After all, it is consistent with the claim that attachment is one mechanism by which what occurs both in and outside the family "gets under the skin" to regulate reproductive development.

Whereas psychosocial acceleration theory emphasized the first 5 to 7 years of life as a sensitive period for the contextual regulation of reproductive strategy, Del Giudice (2009; Del Giudice, Angeleri, & Manera, 2009) drew on sexual selection theory (Trivers, 1972) to highlight the middle-childhood years, contending that this is a period during which the nascent reproductive strategies established in early childhood can be maintained or revised. Of critical importance are peer relations and intrasexual competition—processes, in fact, that appear to mediate effects of environmental context on reproductive strategies (Dishion et al., 2012; James et al., 2012). Indeed, the period during which the adrenal glands mature and sexual feelings first become evident—*adrenarche*—is regarded as a "juvenile transition" and "developmental switch point." One consequence, Del Giudice (2009) has theorized, is the emergence of sex differences in insecure attachment. Although this proposal has been contested by some (van IJzendoorn & Bakermans-Kranenburg, 2010), it will not prove amenable to empirical adjudication until adrenarcheal status, rather than mere chronological age, is measured and its relation to attachment security in middle childhood is determined (Del Giudice & Belsky, 2010).

Beyond attachment, Chisholm (1999) argued that time preference is another important psychological mechanism that is influenced by developmental experiences and regulates reproductive strategy. Theoretically, individuals living in highly risky and uncertain environments should discount the future, preferring smaller payoffs in the present over larger ones later on. In this context, of course, "payoff" refers to the likelihood of reproducing. The fact that children growing up in more economically, socially, and psychologically disadvantaged families find it more difficult than others to wait to secure more attractive rewards and are more inclined to settle for lesser ones sooner (e.g., Evans & English, 2002; Lengua, 2002) seems to be consistent with Chisholm's argument. It remains to be determined, however, whether time preference itself relates to pubertal development or links rearing experience with reproductive functioning.

When it comes to physiological rather than psychological mechanisms of influence, elegant animal research has illuminated an entire epigenetic and developmental cascade that is strikingly consistent with our (Belsky et al., 1991) original theorizing. Indeed, Cameron and her associates (2005) acknowledged just this in a review of their experimental

research showing that the maternal licking and grooming of newborn rat pups, which is itself influenced by stressful or supportive contextual conditions, regulates gene expression and, thereby, stress reactivity, rate of sexual maturation, sexual behavior, and, eventually, parenting (see also Sakhai, Kriegsfeld, & Francis, 2011). The fact that the hypothalamic-pituitary-adrenal axis, among other physiological pathways (Cameron et al., 2008), proved to be an influential link between rearing experience and reproductive development was in line with (a) Chisholm's (1999) speculation that this would be the case, (b) our (Belsky et al., 1991) original proposal that the neuroendocrine system should be explored to better understand how rearing experience influences pubertal development, and (c) Del Giudice and his associates' (2011) new Adaptive Calibration Model of the stress-response system. The fact that licking and grooming does not appear to regulate gene expression and reproductive development in all strains of rat (Kaffman & Meaney, 2007), however, would seem in line with the previous discussed accounts of conditional and alternative reproductive strategies and gene-environment interactions.

Physiologically, fat storage and thus body mass index also merit consideration as mechanisms regulating reproductive strategy (Belsky et al., 1991). This regulatory role seems especially likely given path-analytic evidence linking rearing experience with pubertal development through such mechanisms (Ellis & Essex, 2007; Moffitt, Caspi, Belsky, & Silva, 1992).

Conclusion

Although many social and behavioral scientists continue to regard certain psychological, behavioral, physiological, and somatic developments as "optimal" and others as not, an evolutionary-biological perspective casts many of these supposedly suboptimal developments as alternative means to the same reproductive-fitness-enhancing end. Different developmental processes reflect, ultimately, different strategies that fit different developmental circumstances. As we have seen, this view stimulated an original theory-distinguishing prediction regarding pubertal timing, one that has garnered a good deal of empirical support. Moreover, it has fostered further theory development highlighting (a) the critical importance of harshness and unpredictability as core regulatory dimensions of the environment, (b) adrenarche as an important juvenile switch point, and (c) the fact that individuals likely vary in their developmental susceptibility to contextual regulation.

Taken together, these new issues raise a host of new questions and avenues for inquiry. Are some individuals susceptible to harshness and/or unpredictability only early in life? Are other individuals susceptible to one or both only later in life? And are some people susceptible to both early and late in life, with still others susceptible to neither across the life span? To the extent that these questions can be answered in the affirmative, they would go a long way toward explaining why field

studies have documented environmental effects less powerful than they have long been presumed to be by traditional socialization theory.

Recommended Reading

- Belsky, J., Steinberg, L., & Draper, P. (1991). (See References). The first articulation of the theory of the development of human reproductive strategies which launched the research and additional theory development summarized herein.
- Belsky, J., Steinberg, L., Houts, R. M., Halpern-Felsher, B. L., & The NICHD Early Child Care Research Network. (2010). (See References). Prospective, longitudinal evidence showing that pubertal timing links early rearing with sexual behavior in adolescence.
- Cameron, N. M., Champagne, F. A., Parent, C., Fish, E. W., Osaki-Kuroda, K., & Meaney, M. J. (2005). The programming of individual differences in defensive responses and reproductive strategies in the rat through variations in maternal care. *Neuroscience & Biobehavioral Reviews*, *29*, 843–865. A review of research on rats which illuminates epigenetic and other mechanisms regulating reproductive strategy in accord with theorizing of Belsky et al. (1991).
- Ellis, B. J. (2004). (See References). A masterful, state-of-the-art and theory-informed review of research on influences on female pubertal development.

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