

# 6 The Development of Life History Strategies: Toward a Multi-Stage Theory

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The development of individual differences has always been a primary focus of psychological research, and it continues to be an intensely debated topic to this day. Three issues in particular stand out in contemporary debate. The first pertains to the *sources* of individual variation, with the pressing task of understanding the interplay between genetic and environmental factors. Second, there is the issue of *early experience* (especially within the family) and its role in shaping later development, a role which some question (e.g., Breur, 1999; Harris, 2005) and for which there exists no comprehensive theory capable of accounting for many conflicting findings. Finally comes the issue of *continuity versus discontinuity* in individual differences across the life span; this subject is rendered difficult by the compartmentalized way in which development is often studied and by the lack of organizing principles for linking diverse behavioral phenomena, manifested at different points in time, into meaningful clusters. In this chapter, we illustrate how an evolutionary approach can advance understanding of all three of these issues, and how a developmental perspective can provide fascinating insights to the study of individual differences.

## AN INTEGRATIVE PERSPECTIVE: ADAPTIVE VARIATION IN LIFE HISTORY STRATEGIES

A powerful way of understanding the evolutionary meaning of individual differences is to analyze them in the framework of *strategic* variation (Hagen &

1 Hammerstein, 2005). Different phenotypes can be conceptualized as the  
 2 manifestation of different adaptive strategies, that is, ways for an organism to  
 3 balance costs and benefits in order to maximize its expected fitness (though  
 4 of course this does not imply that *all* individual variation is adaptive). Here  
 5 we focus on a specific kind of strategies, namely, life history (LH) strategies.

## 6 Life-history Strategies

7 Life history theory is a branch of evolutionary biology dealing with the strat-  
 8 egies that organisms use to allocate their limited time and energy to the  
 9 various activities that comprise their life cycle (see Hill, 1993; Kaplan &  
 10 Gangestad, 2005; Chapter 9 of this title). LH theory is essentially concerned  
 11 with identifying optimal solutions—in fitness terms—to various trade-offs,  
 12 the most important of which are that between *somatic effort* (i.e., growth,  
 13 maintenance, and learning) and *reproductive effort*; and, within reproductive  
 14 effort, that between *mating* (i.e., finding and attracting mates) and *parenting*  
 15 (i.e., investing resources in already-born offspring). From another perspec-  
 16 tive, the crucial decisions involved in a LH strategy can be summarized by  
 17 the trade-offs between *current* and *future reproduction*, and between *quality*  
 18 and *quantity of offspring* (see Ellis, Figueredo, Brumbach & Schlomer, 2009).

19 Variation in ecological contexts alters the costs and benefits involved in  
 20 these trade-offs, determining remarkable variation in LH strategies both  
 21 between species and within the same species. A key factor affecting LH strat-  
 22 egies is the pattern of extrinsic mortality; that is, mortality that cannot be  
 23 prevented by altering the organism's behavior. More generally, all (totally or  
 24 partially) uncontrollable factors that negatively affect reproductive success  
 25 can be considered sources of *extrinsic risk* (Quinlan 2007) or, in Ellis and col-  
 26 leagues' (2009) formulation, *extrinsic morbidity-mortality*. When morbidity-  
 27 mortality is high (e.g., because of high pathogen load), it is adaptive to favor  
 28 current reproduction by starting mating early, even at a cost for one's future  
 29 reproductive potential. In addition, high extrinsic risk means that investing  
 30 in parental care has quickly diminishing returns: As (by definition) parental  
 31 effort cannot decrease extrinsic morbidity-mortality, offspring's fitness will  
 32 not respond to parental care beyond a certain amount. Thus, environmental  
 33 risk favors quantity versus quality of offspring and current versus future  
 34 reproduction and selects for life histories that invest in mating at the expense  
 35 of parenting (see Belsky, Steinberg & Draper, 1991; Chisholm 1993;  
 36 Pennington & Harpending 1988). The same effects are caused by increases in  
 37 environment *unpredictability*; by contrast, *resource scarcity* tends to slow down  
 38 development, delay reproduction, and increase parenting effort. Although  
 39 the different components of LH strategies are conceptually distinct, they are  
 40 functionally related and often covary in real-life situations (Ellis et al., 2009);

1 this is why some researchers place LH strategies on a single continuum from  
2 “fast” or *r-selected* (i.e., early maturation and reproduction, quantity over qual-  
3 ity, mating over parenting) to “slow” or *K-selected* (the opposite pattern).

4 Importantly, in sexual species the two sexes predictably differ on most  
5 LH dimensions; they thus can be expected to employ somewhat different  
6 strategies in response to the same environmental cues. In most species, males  
7 tend to engage in higher mating effort and lower parental effort than females  
8 (Geary, 2002; Trivers, 1972). In addition, males usually undergo stronger  
9 sexual selection (i.e., their reproductive success is more variable) and tend to  
10 mature more slowly in order to gain the competitive abilities and qualities  
11 needed for successful competition for mates. Sexual asymmetries in LH  
12 strategies can be attenuated in species with substantial biparental care and  
13 monogamous mating systems. Compared with other mammals, humans  
14 show an unusual degree of paternal investment, and are clearly adapted for  
15 the possibility of monogamous, long-term relationships. However, human  
16 paternal care is highly variable and facultative (e.g., Geary, 2005), and strict  
17 monogamy is rare in human populations (Marlowe, 2000, 2003). Indeed,  
18 human mating is best characterized as strategically flexible (Gangestad &  
19 Simpson, 2000), with a widely documented tendency for men to engage in  
20 higher mating effort than women (e.g., Schmitt, 2005). As a result, the vari-  
21 ous components of LH strategies do not carry the same weight for men and  
22 women. The current vs. future reproduction trade-off is more pressing for  
23 women, since their reproductive rate is limited by the long gestation timing  
24 and the conspicuous energetic investment of pregnancy. In contrast, men can  
25 potentially sire many offspring in a very short time. Men’s crucial trade-off is  
26 that of mating versus parenting: The payoffs of high mating effort are poten-  
27 tially much larger for males, who can benefit directly from having access to a  
28 large number of partners; women can have only one child at a time (twin  
29 pregnancies aside), and thus benefit comparatively less from multiple mat-  
30 ings. Therefore, factors that shift development toward fast LH strategies can  
31 be expected to have a larger impact on reproductive timing in women com-  
32 pared to men, and a larger impact on the mating vs. parenting balance in men  
33 compared to women. Finally, humans can enact “mixed” strategies, where  
34 parental investment and long-term commitment to one’s partner coexists  
35 with the occasional pursuit of short-term matings (see Del Giudice, 2009a;  
36 Gangestad & Simpson, 2000; Jackson & Kirkpatrick, 2007; Schmitt, 2005).

### 37 Developmental Plasticity and the Role of Parental Cues

38 Usually, organisms embody switching mechanisms that allow them to fine-  
39 tune their life histories according to the environmental cues they encounter

1 during development; in other words, LH strategies show *adaptive develop-*  
2 *mental plasticity* (Ellis, Jackson & Boyce, 2006; Chapter 7 of this title; see  
3 West-Eberhard, 2003, for a comprehensive account). Of course, adaptive  
4 plasticity does not entail infinite or arbitrary malleability: Rather, organisms  
5 assess their local environments and adjust their strategic decisions within a  
6 genetically-constrained reaction norm, following evolved rules that tend to  
7 maximize long-term fitness in different ecological conditions.

8 An especially valuable source of information about the local environ-  
9 ment, particularly during the first stages of development, is provided by par-  
10 ents. Parental behavior and parental investment can vary according to the  
11 local ecology, to the parent's own LH strategy, and to offspring condition  
12 (e.g., less investment in low-phenotypic-quality offspring); thus, offspring  
13 can use parents as a source of useful cues about the micro- and macro-  
14 ecological conditions they will (probabilistically) face in the future. This is  
15 especially true when the crucial features of the environment are tolerably  
16 stable, allowing for reliable prediction of future conditions. Even if informa-  
17 tion coming from parents is not completely reliable, offspring—or at least  
18 some offspring (see below)—may be better off not disregarding it, and better  
19 off still by using it, perhaps provisionally, to direct their strategy choice, with  
20 the possibility of later “revision.” So, in long-lived species like humans, one  
21 might expect multi-stage development of LH strategies, whereby individual  
22 strategies remain relatively flexible, rather than becoming fully established  
23 (i.e., fixed) at the beginning of life (Del Giudice, 2009b).

24 On the other hand, the relative unreliability of information about the  
25 future may also select for variation in plasticity, with some genotypes less  
26 responsive to parental cues and more similar to “fixed” strategists (Belsky,  
27 1997a; 2000; 2005; Belsky, Bakermans-Kranenburg & van IJzendoorn, 2007;  
28 Wilson & Yoshimura, 1994). In general, LH theory shows that stochastic  
29 environmental variability tends to increase phenotypic variation (Roff, 2002);  
30 but even in the same environment there may exist different strategies (e.g.  
31 one privileging quantity, another quality) that enjoy equivalent fitness in  
32 the long term. In this case, strategy choice is expected to depend more  
33 strongly on genotypic differences. Mathematical models of plasticity predict  
34 an integration of genetic and environmental determination of individual  
35 strategies (Leimar, Hammerstein & Van Dooren, 2006). More generally,  
36 developmental plasticity coexists with genotypic variation; for example, dif-  
37 ferent genotypes may be more or less plastic or may vary in the threshold  
38 required to switch strategy in response to environmental input (West-  
39 Eberhard, 2003). It may also be that individuals differ in terms of *how long*  
40 they remain open to environmental influences and thus plastic vis-à-vis  
41 reproductive strategy (see Belsky et al., 2007; Belsky & Pluess, 2009). In gen-  
42 eral, human reproductive strategies are likely to show extended plasticity,

1 with a multi-stage developmental process allowing for adjustment and revision,  
 2 depending on the success of one's strategy and on changes in the local  
 3 environmental conditions.

#### 4 Life history Strategies and the Organization of Behavior

5 When interpreted in a narrow sense, LH strategies refer mainly to reproduction-related traits, such as age at first reproduction, fertility, and mating effort.  
 6 However, it is easy to see that the choice of a specific strategy can affect a  
 7 much broader range of traits and behaviors (Belsky et al., 1991; Figueredo  
 8 et al., 2004, 2006; Wolf et al., 2007). Imagine an organism that, following cues  
 9 of environmental risk and unpredictability, adopts a strategy characterized by  
 10 early reproduction and high mating effort. To succeed, the organism needs to  
 11 out-compete same-sex conspecifics and be chosen by members of the other  
 12 sex. Especially for males, this is likely to involve status-seeking behaviors, plus  
 13 considerable investment in traits and displays that the other sex finds attractive  
 14 in short-term mates; in humans, these may involve verbal and creative  
 15 displays, competitive sports, humor, and so on (Jackson & Ellis, 2009; Locke &  
 16 Bogin, 2006; Miller, 2000). Moreover, the cues of environmental risk that  
 17 drive the choice of the strategy will also prompt higher risk-taking in other  
 18 domains (e.g., exploration, fighting, dangerous sexual displays) and a shorter  
 19 time perspective, increasing preference for immediate over delayed rewards  
 20 and impulsivity (Chisholm, 1999a; Daly & Wilson, 2005). Short time perspective  
 21 and competitive attitudes should also decrease the willingness to  
 22 engage in long-term cooperation and to behave altruistically (Belsky et al.,  
 23 1991; Curry, Price & Price, 2008). And since the behaviors associated with a  
 24 fast strategy will predictably increase the organism's expected morbidity-  
 25 mortality, the very fact of having adopted the strategy may act as a  
 26 "self-produced cue" of increased hazard, leading to self-reinforcing feedback  
 27 on behavior.  
 28

29 In synthesis, LH strategies play a powerful role in the organization of  
 30 behavior. We can identify a cluster of related traits that are expected to covary  
 31 along life-history dimensions: mating and sexual strategies, status- and dominance-seeking,  
 32 aggression, cooperation, altruism, risk-taking, time perspective, romantic attachment  
 33 and parenting styles. Correlations within this cluster  
 34 have been documented in both nonhuman animals (e.g., Dingemans &  
 35 Réale, 2005) and in humans (Figueredo et al., 2006). Indeed, Figueredo and  
 36 colleagues (2004, 2005, 2006; Chapter 8 of this title) identified a heritable  
 37 general "*K factor*" accounting for a large proportion of variance in a suite of  
 38 LH-related traits in humans. At the neurobiological level, LH strategies and  
 39 transitions in animals are usually regulated by endocrine mechanisms, with

- 1 sex and stress hormones playing a crucial role (e.g., Adkins-Regan, 2005;
- 2 Hau, 2007; McGlothlin, Jawor & Ketterson, 2007).

### 3 THE DEVELOPMENT OF LIFE HISTORY STRATEGIES

4 In 1991, Belsky and colleagues presented an influential life-history model of  
 5 psychological development, building on Draper and Harpending's (1982)  
 6 work on the effects of father absence on sexual behavior in adolescence and  
 7 young adulthood. A core feature of Belsky et al.'s (1991) model was that  
 8 caregiving behavior (which in turn shapes attachment security) acts as a  
 9 parental cue to the safety and quality of the local environment: Felt security  
 10 in the first 5–7 years would channel the child's developmental trajectory  
 11 along different LH strategies, with secure attachment leading to later repro-  
 12 duction and a quality-oriented style, and insecure attachment leading to  
 13 earlier reproduction and quantity over quality. Furthermore, it was predicted  
 14 that early experiences in the family that would influence felt security also  
 15 would affect the timing of sexual maturation, with children experiencing less  
 16 harmonious parent-child relations and exposed to father absence and/or  
 17 marital conflict reaching puberty earlier than would otherwise be the case.  
 18 Since this model was formulated, several revisions and integrations focused  
 19 specifically on the role of attachment security have been proposed (Belsky,  
 20 1997b, 1999, 2007; Chisholm 1993, 1996, 1999b; Del Giudice, 2009a;  
 21 Kirkpatrick, 1998; Simpson & Belsky, 2008). Here we synthesize the current  
 22 state of the art, focusing on theory and describing key empirical findings  
 23 pertaining to attachment.

#### 24 Parental Cues and the Role of Attachment Security

25 The central idea of these developmental models is that parental behavior  
 26 provides useful information to the child, allowing him/her to adaptively cal-  
 27 ibrate his/her LH strategy. Two basic questions arise: What information? And  
 28 how is the information encoded? Belsky et al. (1991) proposed that rejecting  
 29 or insensitive parenting, often associated with marital discord and broader  
 30 stressful ecological conditions, conveys information about: (1) resource scar-  
 31 city and unpredictability, (2) low levels of social trust and cooperation, and  
 32 (3) instability and low commitment in couple relationships. Chisholm  
 33 (1999b) coined the term "socioassay" to characterize this information the  
 34 child receives about the availability and quality of social relations. Chisholm  
 35 (1993) also argued that the *local mortality rate*, a crucial LH parameter, is a  
 36 key determinant of the quality of caregiving and social relations (see also

1 Bereczkei & Csanaky, 2001), and is thus one of the major pieces of informa-  
2 tion indirectly received by the child.

3 How is all this information encoded? Parental sensitivity, acceptance/  
4 rejection, and familial stress are significant determinants of attachment pat-  
5 terns in infants and children. The general dimension of attachment security  
6 is then well suited to act as a “summary” of the quality and quantity of care-  
7 giving received by the child, which is the reason it figured prominently in  
8 Belsky et al.’s (1991) original model. Closely linked to the stress response  
9 system, the attachment system regulates the child’s feelings of distress, pain,  
10 fear, and loneliness; and while attachment security can change during the  
11 individual’s lifetime, it shows a prototype-like dynamic in which early secu-  
12 rity/insecurity (established in the first few years of life) can continue to affect  
13 behavior into adulthood (Fraley, 2002). Interestingly, insecurely attached  
14 adults have been found to report shorter estimates of their own life expect-  
15 tancy (Chisholm, 1999a), thus supporting the hypothesized link between  
16 attachment security and perceived environmental harshness.

17 While generally accurate, this outline needs some conceptual revisions.  
18 First, the models advanced by Belsky et al. (1991) and Chisholm (1999b)  
19 conflated the negative dimensions of the environment in a single, undifferen-  
20 tiated factor including risk, unpredictability and resource scarcity. Modern  
21 life history theory, however, suggests that different aspects of the environ-  
22 ment may have different (even opposing) effects on LH strategies. Whereas  
23 extrinsic morbidity-mortality and unpredictability should shift strategies  
24 toward current reproduction and mating effort, as postulated in the original  
25 models, severe resource scarcity per se may actually have the opposite effect,  
26 favoring slow life histories and substantial biparental investment in children  
27 (see Ellis et al. 2009; Marlowe, 2000, 2003).

28 Second, maternal and paternal investment (and, consequently, attach-  
29 ment to mother and father) may provide the child with distinctive informa-  
30 tion about the environment (Del Giudice, 2009a); indeed, Ellis (2004) has  
31 long granted, following Draper and Harpending (1982), a special role for the  
32 father. Although data remain scarce, anthropological evidence suggests that  
33 maternal caregiving is more directly tied to environmental harshness than its  
34 paternal counterpart, which may be more dependent on mating system (e.g.  
35 polygyny vs. monogamy), the local sex ratio, and the intensity of male-male  
36 competition for status (Blurton Jones et al., 2000; Quinlan, 2007; Quinlan &  
37 Quinlan, 2007).

38 Third, parents may invest little in a given child because of “micro-  
39 ecological” factors such as parent’s mental illness, low phenotypic quality of  
40 the child, or the presence of step-parents. Even though such factors contrib-  
41 ute to insecure attachment and early stress, they do not strictly convey infor-  
42 mation about the “macro-ecological” context à la Belsky et al. (1991); they

1 may actually provide information about the likelihood of receiving future  
2 investment by one's own family (Ellis, 2004; Del Giudice, 2009a).

3 Perhaps due to the imperfect reliability of parental behavior as a source  
4 of information or the fact that having one's development shaped by parent-  
5 ing may prove maladaptive in fitness terms, children differ in their sensitivity  
6 to the early familial environment (Belsky, 1997b, 2005; Belsky et al., 2007;  
7 Belsky & Pluess, 2009). Indeed, there are evolutionary grounds for hypothe-  
8 sizing that some children would be "fixed strategists" pursuing a particular  
9 LH strategy almost irrespective of their developmental experiences, whereas  
10 others would be "plastic strategists" pursuing conditional strategies strongly  
11 shaped by their developmental experiences. Consistent with this is emerging  
12 evidence that infants and toddlers with a highly reactive and negatively emo-  
13 tional temperament tend to be more affected by parenting than other chil-  
14 dren (reviewed in Belsky, 2005; see also Bradley & Corwyn, 2008), as do  
15 children carrying a particular dopamine receptor D4 allele (7-repeat *DRD4*;  
16 Bakermans-Kranenburg & Van IJzendoorn, 2006) or alleles associated with  
17 low monoamine oxidase A (MAOA) activity (Caspi et al., 2002). These chil-  
18 dren appear to be more positively affected by nurturing and supportive rear-  
19 ing environments, as well as more negatively affected by harsh and  
20 unsupportive ones. Recently, another important genotype-by-environment  
21 (GxE) interaction involving attachment security in infants was discovered by  
22 Barry, Kochanska, and Philibert (2008). Whereas infants with one or two  
23 short alleles on the serotonin transporter gene (*5-HTT*) were affected, as  
24 expected, by maternal sensitivity, so that low sensitivity led to attachment  
25 insecurity, virtually all of those carrying two long alleles became securely  
26 attached irrespective of the quality of care experienced.

27 While genotypic factors may account for variable plasticity in response to  
28 parental influence, Boyce and Ellis (2005; Ellis, Essex & Boyce, 2005) have  
29 argued that children's environmental sensitivity, which they label *biological*  
30 *sensitivity to context*, could itself be affected (at least in part) by the experience  
31 of early stress. In their model, high stress reactivity (viewed as a more plastic  
32 phenotype) would be adaptive both in supportive/favorable environments,  
33 where it would increase susceptibility to social and developmental benefits, and  
34 in very stressful/unfavorable environments, where it would prompt increased  
35 vigilance to danger and threats. This proposal is very interesting, and the idea  
36 that plasticity can be environmentally induced is definitely worth pursuing.

### 37 Stages, Transitions, and Extended Plasticity

38 We propose that human LH strategies develop in a flexible, multi-stage fash-  
39 ion. As already anticipated in the original formulation by Belsky et al. (1991),

1 enduring effects of early influences could be contingent on later ones, mean-  
2 ing that LH strategies would remain open, to some extent, to continual  
3 modification, though perhaps for some people more than others. A sequen-  
4 tial process of assessment-adjustment could provide the best compromise  
5 between early commitment to a strategy (with the benefit of having time to  
6 develop the appropriate skills) and finely tuned tracking of changes in eco-  
7 logical and social conditions. In this process, it should be possible to identify  
8 some *developmental switch points* (see West-Eberhard, 2003; Ellis, Jackson &  
9 Boyce, 2006; Del Giudice et al., in press) when plasticity is preferentially  
10 expressed and development is directed (or re-directed) along alternative  
11 pathways. At developmental switch points, genotypic variation is integrated  
12 with information from the environment (West-Eberhard, 2003), and the  
13 result of this integration shapes strategy “choice.”

14 What are the switch points in the development of human LH strategies?  
15 The answer is still partial, but our map is becoming more detailed (Figure  
16 6.1). To begin with, some preliminary strategy-setting (affecting, for exam-  
17 ple, the degree of temperamental reactivity) may occur even before birth, for  
18 example following exposure to maternal stress hormones. Then, in the first  
19 years of life (when dependency on parents is maximal), attachment security  
20 can provide the child with indirect information about the local micro- and  
21 macro-ecology, thus entraining the development of conditional strategies.  
22 But when do these nascent LH strategies begin to be effectively implemented  
23 in children’s behavior?

## 24 The Juvenile Transition

25 Del Giudice (2009a; Del Giudice, Angeleri & Manera, 2009) argued that the  
26 first crucial switch point translating early stress into behavioral strategies  
27 coincides with the transition from early to middle childhood, labeled the  
28 *juvenile transition*, immediately following what Belsky et al. (1991) identified  
29 as essentially the sensitive period for establishing the nascent LH strategy.  
30 With the juvenile transition (which takes place around 6–8 years in industri-  
31 alized societies), children dramatically increase their participation in social  
32 activities with peers, and they begin to effectively compete for place in dom-  
33 inance hierarchies and for ranking as socially attractive individuals. Middle  
34 childhood is characterized by a dramatic increase in competitive and social  
35 play (Pellegrini & Archer, 2005; Smith et al., 2005), by the onset of the first  
36 romantic (and sometimes sexual) attractions (Herdt & McClintock, 2000),  
37 and more generally by a peak in sexually differentiated behavior (Geary,  
38 1998).

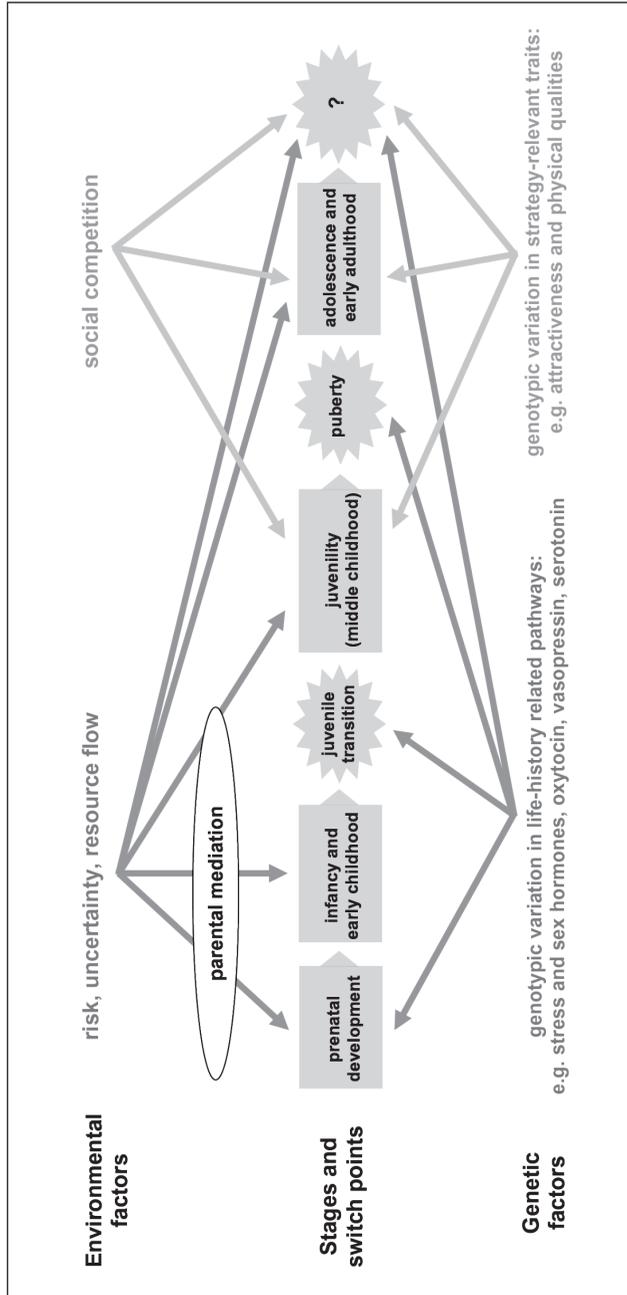


Figure 6.1 Stages and switch points in the development of human life history strategies.

1 The functional role of the juvenile transition vis-à-vis life history strate-  
2 gies is threefold: first, it co-ordinates the phenotypic expression of a suite of  
3 life history-related traits, including attachment, stress regulation, dominance  
4 seeking, cooperation, and nascent sexuality. Second, it does so in a sexually-  
5 differentiated way; for example, a mating-oriented strategy is expected to  
6 prompt an increase in high-risk, physically aggressive dominance-seeking in  
7 boys more than in girls (see below). Finally, human juvenility (i.e., middle  
8 childhood) provides an assessment period before the actual onset of mating  
9 and reproduction; such an assessment period may be crucial for appraising  
10 the likely success of a chosen strategy, prompting strategic revision in case  
11 the strategy is unsuccessful or does not match the child's social environment  
12 (Del Giudice, 2009b). Consistent with this claim is evidence that the degree  
13 of agonistic stress experienced in early adolescence affects the choice of  
14 mating strategies in adulthood (Davis & Werre, 2007). The intensity of social  
15 competition and the levels of trust, cooperation and aggression in one's peer  
16 environment should be important factors contributing to the development  
17 of LH strategies in juvenility and adolescence.

18 When life history-related behavioral strategies are played out in the peer  
19 group, the relevant phenotypic traits become crucial in determining the out-  
20 comes: intelligence, attractiveness, and physical qualities such as strength and  
21 athletic prowess are required in different proportions by different strategies.  
22 Jackson and Ellis (2009) proposed that, especially for males, the social status  
23 acquired in adolescence (partly depending on one's phenotype) should be a  
24 critical factor affecting the development of LH strategies. This approach is  
25 fully consistent with the model we present, although the critical phase of  
26 social feedback may already begin with juvenility.

27 Del Giudice and colleagues (2009) contend that the juvenile transition  
28 is mediated by the hormonal mechanism of "adrenal puberty" or *adrenarche*  
29 (the secretion of androgens<sup>1</sup> by the adrenal gland, beginning at about  
30 6–8 years in industrialized countries; see Auchus & Rainey, 2004; Ibáñez  
31 et al., 2000). Adrenarche would act as a plasticity regulator, by integrating  
32 genetic and environmental information and shaping the expression of both  
33 sex-related and individual differences. From this perspective, life history  
34 strategies are primarily coordinated by a dynamic interplay of the stress  
35 and sexual endocrine pathways, with various neurobiological systems (e.g.  
36 the serotonergic system) being involved in their behavioral expression  
37 and fine-tuned regulation. The outcome of this hypothesized process is the

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<sup>1</sup> The main adrenal androgens are dehydroepiandrosterone (DHEA) and dehydroepiandrosterone sulfate (DHEAS), two chemical precursors of testosterone and estradiol that can be converted to active androgens and estrogens in the CNS (e.g., Labrie et al., 2001).

1 emergence of coordinated individual and sex-related differences in the func-  
2 tioning of the stress system, the sexual system, and many behavioral systems  
3 directly or indirectly affected by them. This working model of the juvenile  
4 transition remains speculative in many respects, although much evidence is  
5 consistent with it: Del Giudice and colleagues (2009) summarize a number  
6 of empirical studies showing that the juvenile transition is linked to develop-  
7 mental discontinuity in aggression levels, and to the onset of anxiety- and  
8 aggression-related psychological disorders. Finally, a recent longitudinal study  
9 by Ellis and Essex (2007) found that early familial stress anticipates adrenar-  
10 che in both males and females, consistent with the role we propose for  
11 adrenarche as a life-history switch point.

## 12 Puberty

13 The next switch point is provided by puberty, when individuals first enter  
14 the arena of actual mating and reproduction. The original prediction by  
15 Belsky and colleagues (1991) was that early stress would lead to earlier onset  
16 of puberty, as part of a strategy oriented to current reproduction. Following  
17 Draper and Harpending's (1982) emphasis on father absence, many research-  
18 ers have focused their puberty research on the effects of father absence and  
19 family structure on age at menarche, even though a central premise of Belsky  
20 et al.'s (1991) model was that the child should be sensitive to more than  
21 just the presence/absence of father when it comes to calibrating a reproduc-  
22 tive strategy.<sup>2</sup> There are now several studies assessing stressful family  
23 relationships more generally and looking at puberty timing in both sexes  
24 (see Belsky et al., 2007; Tither & Ellis, 2008 for reviews). The overall result  
25 of this evolutionary-inspired developmental research is that stressful and  
26 negative family relationships do seem to accelerate the onset of puberty (but  
27 only in girls; Belsky et al., 2007), and to predispose to earlier initiation of  
28 sexual activity. Fathers may play an especially important, even if not exclu-  
29 sive, role (Ellis, 2004; Quinlan, 2003); father absence *per se*, however, may  
30 not be the most important factor, since father's psychosocial adjustment and  
31 parental investment appear to exert a sizeable moderating effect, consistent  
32 with Belsky et al.'s (1991) original theorizing. What is still debated is the  
33 extent to which the putative environmental influences being detected are  
34 genetically mediated or accounted for (e.g., Mendle et al., 2006, 2008; Rowe,  
35 2000), though recent genetically-informed research indicates that this is  
36 by no means entirely the case (D'Onofrio et al., 2006; Ellis & Essex, 2007;

<sup>2</sup> Other studies suggest that stepfather presence could have a specific role in predicting early menarche (see Ellis, 2004; Mendle et al., 2006).

1 Tither & Ellis, 2008). In fact, even studies highlighting the genetic mediation  
 2 of environmental influences may ultimately be consistent with the notion  
 3 that, within a family, children vary in the extent to which their LH strategies  
 4 are fixed or plastic (that is, developmentally regulated by family processes;  
 5 Belsky, 2005).

6 Another important issue concerning puberty is the changing function  
 7 of attachment when individuals enter reproductive age. Whereas attach-  
 8 ment in childhood is primarily devoted to promoting survival (by securing  
 9 parental investment and protection), in adults the attachment system serves  
 10 a different evolutionary function—regulating long-term bonding between  
 11 reproductive partners (Kirkpatrick, 1998; Jackson & Kirkpatrick, 2007).  
 12 Whereas attachment in childhood plays the role of a key factor affecting the  
 13 development of *nascent* LH strategies, in adulthood it becomes *part* of the  
 14 individual's manifest strategy.

## 15 Adulthood

16 Life history trade-offs extend well beyond puberty, and it seems likely that  
 17 other switch points can be found across the human life course. For example,  
 18 menopause most certainly represents a fundamental switch point for women,  
 19 and there seems to be a tendency for men around the world to increase their  
 20 parental effort when approaching middle age (Winking et al., 2007). Other  
 21 factors may also contribute to strategic adjustment during adult life, even  
 22 without qualifying as identifiable “switch points.” An event of special signifi-  
 23 cance may be represented by the birth of one's child: Not only does it signal  
 24 (some degree of) reproductive success, but it is known to affect hormonal  
 25 functioning in both sexes (e.g., Storey et al., 2000), and could thus directly  
 26 interact with the endocrine systems which, in our model, regulate LH strate-  
 27 gies. Dramatic changes in social dominance (especially for men) and in social  
 28 support (especially for women) may also act as triggers for recalibrating one's  
 29 strategy in response to changing opportunities in the environment.

## 30 Sex Differences in Life History Strategies

31 When it comes to LH strategies, the sexes differ both in their available stra-  
 32 tegic options and in the related fitness costs and benefits. For this reason, the  
 33 mechanisms regulating strategic variation are not sexually monomorphic and  
 34 the same cues may exert quite different effects depending on the person's  
 35 sex. What happens when environmental cues (e.g. rejecting parenting) signal  
 36 elevated risk? In general, we expect LH strategies to shift toward present-  
 37 oriented reproduction (i.e., early maturation, early sexual debut), increased  
 38 mating, and reduced parental investment. However, there are reasons to

1 expect males to adopt high-mating strategies even at moderate levels of risk  
2 (if able to mate with many partners), whereas females would favor higher  
3 investment levels in their offspring. Only at high levels of risk are females  
4 expected to adopt a male-like high-mating, low-parenting strategy (see Del  
5 Giudice, 2009a). Consistent with this account, romantic attachment styles in  
6 adults often show predictable sex differences, with males reporting higher  
7 levels of *avoidant* (dismissing) attachment, and females reporting higher  
8 levels of *anxious* (preoccupied, ambivalent) attachment. This pattern is con-  
9 sistenty found in community samples, whereas studies of undergraduates  
10 seem to yield smaller effects (see Del Giudice, 2009b; Del Giudice & Belsky,  
11 2010). Sex-biased distributions of attachment have been found cross-  
12 culturally; across geographical regions, increased environmental risk predicts  
13 higher levels of avoidance, especially in females, and tends to reduce within-  
14 population sex differences (Schmitt et al., 2003). Avoidant attachment bears  
15 the hallmarks of a low-parenting strategy, favoring short-term relationship  
16 over intimate, long-term bonding (Belsky, 1997b; Kirkpatrick, 1998):  
17 Avoidant adults are more promiscuous and sexually unrestrained, less com-  
18 mitted in couple relationships, tend to avoid intimacy, and are more likely to  
19 become sexually coercive (e.g., Allen & Baucom, 2004; Bogaert & Sadava,  
20 2002; Brassard et al., 2007; Gentzler & Kerns, 2004). They report lower  
21 interest in long-term relationships (Jackson & Kirkpatrick, 2007), and tend to  
22 feel more attracted by persons other than the current partner (Overall &  
23 Sibley, 2008).

24 In contrast, anxious adults show higher dependency and are powerfully  
25 motivated to search for exclusive, intimate relationships. Whereas attach-  
26 ment anxiety in men is related to somewhat reduced mating success, in  
27 women it predicts earlier sexual debut, impulsive partner choice, and infidel-  
28 ity (see references above). Del Giudice (2009a) proposed that anxious  
29 attachment in women has been selected as a care-eliciting strategy, targeted  
30 at extracting continued investment and help from both partners and rela-  
31 tives. Attachment anxiety could play the role of a “counter-strategy” to male  
32 avoidance at moderate levels of risk. Moreover, both avoidant and anxious  
33 styles could predispose women to multiple, impulsive matings—consistent  
34 with the evolutionary hypothesis that women possess a conditional strategy  
35 of “facultative polyandry” (see Hrdy, 2000).

36 Sex differences in attachment styles are not only present in adults; nota-  
37 bly, they seem to emerge during the juvenile transition, that is, around seven  
38 years of age (Del Giudice, 2008, 2009b; but see Bakermans-Kranenburg &  
39 van IJzendoorn [2009], and the response by Del Giudice & Belsky, in press).  
40 The emergence of sex differences in middle childhood is a crucial link between  
41 early attachment and adult mating styles; since they are found with respect to  
42 child-*parent* relationships, they support the idea of a global reorganization of

1 the attachment system in the transition from childhood to adulthood.  
2 According to Del Giudice (2009a; Del Giudice et al., 2009), sex-biased  
3 attachment patterns in juvenility are part of a more general sexual differen-  
4 tiation of LH strategies. Avoidant attachment in children is related to pseudo-  
5 maturity, overt/physical aggression, inflated self-esteem, and externalizing  
6 symptoms. These traits may be functional as part of a high-risk, dominance-  
7 oriented male strategy oriented at gaining status and prominence in the  
8 peer group. In contrast, anxious attachment could function for females as a  
9 means of keeping oneself in close contact with the kin network  
10 (Del Giudice, 2009a; Goetz, Perilloux & Buss, 2009); more speculatively,  
11 emphasizing immaturity and dependency might work as an attractiveness dis-  
12 play directed at males (Marquez & Rucas, 2008). In addition, attachment  
13 anxiety may predict increased relational/indirect aggression in the context of  
14 female peer competition (Campbell, 2009; Del Giudice, 2009b), but since  
15 most attachment-aggression studies have focused on overt physical aggres-  
16 sion, this intriguing possibility remains to be explored. Finally, insecure attach-  
17 ment in juvenility predicts the early appearance of flirting and sexual contacts,  
18 even in pre-pubertal children (Sroufe et al., 1993); this further underlines the  
19 emerging functional coupling of the attachment and sexual systems.  
20

### Integration with Neurobiology

21  
22 The present account of the development of attachment and LH strategies fits  
23 nicely with two recent neurobiological models of the stress response. Taylor  
24 et al. (2000) convincingly argued that the mammalian stress system works in  
25 a sexually dimorphic way: The classical “fight-or-flight” response is more  
26 typical of males, whereas females tend to manifest a “tend-and-befriend”  
27 response, characterized by protection of one’s offspring and increased affilia-  
28 tive behaviors. The “fight-or-flight” versus “tend-and-befriend” distinction  
29 closely mirrors the difference between (male-typical) avoidant and (female-  
30 typical) anxious insecure attachment, the latter being characterized by  
31 increased dependency and closeness-seeking.

32 Also relevant to our multi-stage theory of the development of reproduc-  
33 tive strategies is Korte et al.’s (2005) “hawk-dove” model which regards indi-  
34 vidual variability in the physiology of the stress response as contingent on two  
35 alternative phenotypes. The aggressive “hawk” strategy is characterized by  
36 fight-or-flight behaviors, high androgen levels, low cortisol secretion, and high  
37 sympathetic/low parasympathetic activation. In contrast, the “dove” strategy  
38 is marked by freeze-hide behaviors and an opposite neurobiological profile;  
39 the two strategies are also hypothesized to be associated with different  
40 profiles in serotonin, dopamine, and vasopressin functionality. We think that

1 the “hawk” phenotype could describe the stress response pattern of avoidant  
 2 individuals (especially males): The interplay between stress and sex hormones  
 3 during development may entrain a developmental pathway in which early  
 4 insecure attachment interacts with androgen secretion via multiple feedbacks,  
 5 leading to a profile of high androgen levels, lowered stress responsivity (e.g.  
 6 lower cortisol secretion), and high aggression and impulsivity.  
 7

## CONCLUSION

8  
 9 A great promise of the life history framework is its capacity to dramatically  
 10 increase *integration* in the study of individual differences from a developmen-  
 11 tal perspective. There is, first, integration across life stages: Thinking of  
 12 development as a sequence of switch points, with each phase linked to spe-  
 13 cific evolutionary functions, resolves the contradiction between continuity  
 14 and discontinuity in development by relating them in the same explanatory  
 15 frame. Next there is integration across behavioral domains: LH theory makes  
 16 sense of covariation among different traits and behaviors, thus contributing  
 17 to one of the main goals of individual differences psychology. Finally, this  
 18 perspective permits increased integration between genetic and environmen-  
 19 tal determination of individual differences via the concept of developmental  
 20 plasticity. The emerging map we have tried to draw highlights a fascinating  
 21 and intricate landscape, full of uncharted pathways and opportunities for  
 22 discovery; we anticipate that, in the next future, the development of indi-  
 23 vidual differences will become a productive and informative focus of inquiry  
 24 in evolutionary psychology at large.

## REFERENCES

- 25  
 26 Adkins-Regan, E. (2005). *Hormones and animal social behavior*. Princeton,  
 27 NJ: Princeton University Press.  
 28 Allen, E. S., & Baucom, D. H. (2004). Adult attachment and patterns of  
 29 extradyadic involvement. *Family Process, 43*, 467–488.  
 30 Auchus, R.J., & Rainey, W.E. (2004). Adrenarche—physiology, biochemistry  
 31 and human disease. *Clinical Endocrinology, 60*, 288–296.  
 32 Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2006). Gene-  
 33 environment interaction of the dopamine D4 receptor (DRD4) and  
 34 observed maternal insensitivity predicting externalizing behavior in pre-  
 35 schoolers. *Developmental Psychobiology, 48*, 406–409.

- 1 Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2009). No reliable  
2 gender differences in attachment across the life-span. *Behavioral and*  
3 *Brain Sciences*, 32, 22–23.
- 4 Barry, R.A., Kochanska, G., & Philibert, R.A. (2008). G X E interactions in  
5 the organization of attachment: Mothers' responsiveness as a moderator  
6 of children's genotypes. *Journal of Child Psychology and Psychiatry*, 49,  
7 1313–1320.
- 8 Belsky, J. (1997a). Attachment, mating, and parenting: An evolutionary inter-  
9 pretation. *Human Nature*, 8, 361–381.
- 10 Belsky, J. (1997b). Theory testing, effect-size evaluation and differential sus-  
11 ceptibility to rearing influence: The case of mothering and attachment.  
12 *Child Development*, 64, 598–600.
- 13 Belsky, J. (1999). Modern evolutionary theory and patterns of attachment.  
14 In J. Cassidy & P. Shaver (Eds.), *Handbook of attachment: Theory and re-*  
15 *search* (pp. 151–173). New York: Guilford.
- 16 Belsky, J. (2000). Conditional and alternative reproductive strategies:  
17 Individual differences in susceptibility to rearing experience. In J. Rodgers,  
18 D. Rowe, & W. Miller (Eds.), *Genetic influences on human fertility and*  
19 *sexuality: Theoretical and empirical contributions from the biological and*  
20 *behavioral sciences* (pp. 127–146). Boston: Kluwer.
- 21 Belsky, J. (2005). Differential susceptibility to rearing influence: An evolu-  
22 tionary hypothesis and some evidence. In B. Ellis & D. Bjorklund (Eds.),  
23 *Origins of the social mind: Evolutionary psychology and child development*  
24 (pp. 139–163). NY: Guilford.
- 25 Belsky, J. (2007). Childhood experiences and reproductive strategies. In  
26 R. Dunbar & L. Barrett (Eds.), *Oxford handbook of evolutionary psychol-*  
27 *ogy* (pp. 237–254) Oxford, UK: Oxford University Press.
- 28 Belsky, J., Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2007). For  
29 better *and* for worse: differential susceptibility to environmental influ-  
30 ences. *Current Directions in Psychological Science*, 16, 300–304.
- 31 Belsky, J., & Pluess, M. (2009). The nature (and nurture?) of plasticity in  
32 human development. *Perspectives in Psychological Science*, 4, 345–351.
- 33 Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interper-  
34 sonal development, and reproductive strategy: an evolutionary theory of  
35 socialization. *Child Development*, 62, 647–670.
- 36 Bereczkei, T., & Csanaky, A. (2001). Stressful family environment, mortality,  
37 and child socialisation: Life-history strategies among adolescents and  
38 adults from unfavourable social circumstances. *International Journal of*  
39 *Behavioral Development*, 25, 501–508.
- 40 Blurton Jones, N. G., Marlowe, F. W., Hawkes, K., & O'Connell, J. F. (2000).  
41 Paternal investment and hunter-gatherer divorce rates. In L. Cronk,

- 1 N. Chagnon, & W. Irons, (eds.), *Adaptation and human behavior: An anthropological perspective*, pp. 69–90. New York: Aldine De Gruyter.
- 2
- 3 Bogaert, A. F., & Sadava, S. (2002). Adult attachment and sexual behavior.
- 4 *Personal Relationships*, 9, 191–204.
- 5 Boyce, W. T., & Ellis, B. J. (2005). Biological sensitivity to context: I. An evolutionary-developmental theory of the origins and functions of stress
- 6 reactivity. *Development and Psychopathology*, 17, 271–301.
- 7
- 8 Bradley, R. H., & Corwyn, R. F. (2008). Infant temperament, parenting, and
- 9 externalizing behavior in first grade: a test of the differential susceptibility
- 10 hypothesis. *Journal of Child Psychology and Psychiatry and Allied*
- 11 *Disciplines*, 49, 124–131.
- 12 Brassard, A., Shaver, P. R., & Lussier, Y. (2007). Attachment, sexual experience, and sexual pleasure in romantic relationships: a dyadic approach.
- 13 *Personal Relationships*, 14, 475–49.
- 14
- 15 Breur, J. T. (1999). *The myth of the first three years*. New York: Free Press.
- 16 Campbell, A. (2009). “Fatal attraction” syndrome: not a good way to keep
- 17 your man. *Behavioral and Brain Sciences*, 32, 24–25.
- 18 Caspi, A., McClay, J., Moffitt, T. E., Mill, J., Martin, J., Craig, I. W., et al.
- 19 (2002). Role of genotype in the cycle of violence in maltreated children.
- 20 *Science*, 297, 851–854.
- 21 Chisholm, J. S. (1993). Death, hope, and sex: life-history theory and the
- 22 development of reproductive strategies. *Current Anthropology*, 34, 1–24.
- 23 Chisholm, J. S. (1996). The evolutionary ecology of attachment organization.
- 24 *Human Nature*, 7, 1–38.
- 25 Chisholm, J. S. (1999a). Attachment and time preference: Relations between
- 26 early stress and sexual behavior in a sample of American university
- 27 women. *Human Nature*, 10, 51–83.
- 28 Chisholm, J. S. (1999b). *Death, hope and sex: steps to an evolutionary ecology*
- 29 *of mind and morality*. New York: Cambridge University Press.
- 30 Crawford, T. N., Shaver, P. R., Cohen, P., Pilkonis, P. A., Gillath, O., &
- 31 Kasen, S. (2006). Self-reported attachment, interpersonal aggression,
- 32 and personality disorder in a prospective community sample of adolescents
- 33 and adults. *Journal of Personality Disorders*, 20, 331–351.
- 34 Curry, O. S., Price, M. E., & Price, J. G. (2008). Patience is a virtue: cooperative
- 35 people have lower discount rates. *Personality and Individual*
- 36 *Differences*, 44, 780–785.
- 37 Daly, M., & Wilson, M. (2005). Carpe diem: Adaptation and devaluing the
- 38 future. *The Quarterly Review of Biology*, 80, 55–60.
- 39 Davis, J., & Werre, D. (2007). Agonistic stress in early adolescence and its
- 40 effects on reproductive effort in young adulthood. *Evolution and Human*
- 41 *Behavior*, 28, 228–233.

- 1 Del Giudice, M. (2009a). Sex, attachment, and the development of repro-  
 2 ductive strategies. *Behavioral and Brain Sciences*, 1–67.
- 3 Del Giudice M. (2009b). Human reproductive strategies: An emerging syn-  
 4 thesis? *Behavioral and Brain Sciences*, 45–67.
- 5 Del Giudice, M. (2008). Sex-biased distribution of avoidant/ambivalent  
 6 attachment in middle childhood. *British Journal of Developmental*  
 7 *Psychology*, 26, 369–379.
- 8 Del Giudice, M., Angeleri, R., & Manera, V. (2009). The juvenile transition:  
 9 A developmental switch point in human life history. *Developmental*  
 10 *Review*, 29, 1–31.
- 11 Del Giudice, M., & Belsky, J. (in press). Sex differences in attachment emerge  
 12 in middle childhood: An evolutionary hypothesis. *Child Development*  
 13 *Perspectives*.
- 14 Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal person-  
 15 ality. *Behaviour*, 142, 1165–1190.
- 16 D’Onofrio, B. M., Turkheimer, E., Emery, R. E., Slutske, W. S., Heath, A. C.,  
 17 Madden, P. A., & Martin, N. G. (2006). A genetically informed study of  
 18 the processes underlying the association between parental marital insta-  
 19 bility and offspring adjustment. *Developmental Psychology*, 42, 486–499.
- 20 Draper, P., & Harpending, H. (1982). Father absence and reproductive strat-  
 21 egy: an evolutionary perspective. *Journal of Anthropological Research*, 38,  
 22 255–273.
- 23 Ellis, B. J. (2004). Timing of pubertal maturation in girls: An integrated life  
 24 history approach. *Psychological Bulletin*, 130, 920–958.
- 25 Ellis, B.J., & Essex, M.J. (2007). Family environments, adrenarche and sexual  
 26 maturation: A longitudinal test of a life history model. *Child Development*,  
 27 78, 1799–1817.
- 28 Ellis, B. J., Essex, M. J., & Boyce, W. T. (2005). Biological sensitivity to context:  
 29 II. Empirical explorations of an evolutionary-developmental theory.  
 30 *Development and Psychopathology*, 17, 303–328.
- 31 Ellis, B. J., Jackson, J. J., & Boyce, W. T. (2006). The stress response system:  
 32 universality and adaptive individual differences. *Developmental Review*,  
 33 26, 175–212.
- 34 Ellis, B. J., Figueredo, A. J., Brumbach, B. H. & Schlomer, G. L. (2009). The  
 35 impact of harsh versus unpredictable environments on the evolution and  
 36 development of life history strategies. *Human Nature*, 20, 204–268.
- 37 Figueredo, A. J., Vásquez, G., Brumbach, B. H. & Schneider, S. M. R. (2004).  
 38 The heritability of life history strategy: The K-factor, covitality, and per-  
 39 sonality. *Social Biology*, 51, 121–143.
- 40 Figueredo, A. J., Vásquez, G., Brumbach, B., Sefcek, J. A., Krisner, B. R., &  
 41 Jacobs, W. J. (2005). The K-factor: Individual differences in life-history  
 42 strategy. *Personality and Individual Differences*, 39, 1349–1360.

- 1 Figueredo, A. J., Vásquez, G., Brumbach, B., Schneider, S. M. R., Sefcek, J. A.,  
 2 Tal, I. R.,... Jacobs, W. J. (2006). Consilience and life history theory: from  
 3 genes to brain to reproductive strategy. *Developmental Review*, 26,  
 4 243–275.
- 5 Fraley, R. C. (2002). Attachment stability from infancy to adulthood: meta-  
 6 analysis and dynamic modeling of developmental mechanisms. *Personality  
 7 and Social Psychology Review*, 6, 123–151.
- 8 Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating:  
 9 trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, 23,  
 10 573–587.
- 11 Geary, D. C. (1998). *Male, female. The evolution of human sex differences*.  
 12 Washington, DC: American Psychological Association.
- 13 Geary, D. C. (2002). Sexual selection and human life history. *Advances in  
 14 Child Development and Behavior*, 30, 41–101.
- 15 Geary, D. C. (2005). Evolution of paternal investment. In D. M. Buss (Ed.),  
 16 *The evolutionary psychology handbook* (pp. 483–505). Hoboken, NJ:  
 17 John Wiley & Sons.
- 18 Gentzler, A. L., & Kerns, K. A. (2004). Associations between insecure attach-  
 19 ment and sexual experiences. *Personal relationships*, 11, 249–265.
- 20 Goetz, C. D., Perilloux, C., & Buss, D. M. (2009). Attachment strategies across  
 21 sex, time, and relationship type. *Behavioral and Brain Sciences*, 32, 28–29.
- 22 Hagen, E. H., & Hammerstein, P. (2005). Evolutionary biology and the strate-  
 23 gic view of ontogeny: genetic strategies provide robustness and flexibility  
 24 in the life course. *Research in Human Development*, 2, 87–101.
- 25 Harris, J. R. (2005). Social behavior and personality development. In B. J. Ellis  
 26 & D. F. Bjorklund, (eds.), *Origins of the social mind: evolutionary psychol-  
 27 ogy and child development*, pp. 245–270. New York: Guilford.
- 28 Hau, M. (2007). Regulation of male traits by testosterone: implications for  
 29 the evolution of vertebrate life histories. *BioEssays*, 29, 133–144.
- 30 Herdt, G., & McClintock, M. (2000). The magical age of 10. *Archives of  
 31 Sexual Behavior*, 29, 587–606.
- 32 Hill, K. (1993). Life history theory and evolutionary anthropology.  
 33 *Evolutionary Anthropology*, 2, 78–88.
- 34 Hrdy, S. B. (2000). The optimal number of fathers: evolution, demography,  
 35 and history in the shaping of female mate preferences. *Annals of the New  
 36 York Academy of Sciences*, 907, 75–96.
- 37 Ibáñez, L., Dimartino-Nardi, J., Potau, N., & Saenger, P. (2000). Premature  
 38 adrenarche – normal variant or forerunner of adult disease? *Endocrine  
 39 Reviews*, 21, 671–696.
- 40 Jackson, J. J., & Ellis, B. J. (2009). Synthesizing life history theory with sexual  
 41 selection: Toward a comprehensive model of alternative reproductive  
 42 strategies. *Behavioral and Brain Sciences*, 32, 31–32.

- 1 Jackson, J. J., & Kirkpatrick, L. A. (2007). The structure and measurement of  
 2 human mating strategies: towards a multidimensional model of socio-  
 3 sexuality. *Evolution and Human Behavior*, 28, 382–391.
- 4 Kaplan, H. S., & Gangestad, S. W. (2005). Life history theory and evolution-  
 5 ary psychology. In D. M. Buss (Ed.) *Handbook of evolutionary psychology*  
 6 (pp.68–95). New Jersey: Wiley.
- 7 Kirkpatrick, L. A. (1998). Evolution, pair bonding, and reproductive strate-  
 8 gies: a reconceptualization of adult attachment. In J. A. Simpson & W. S.  
 9 Rholes, (eds.), *Attachment theory and close relationships*, pp. 353–393.  
 10 New York: Guilford.
- 11 Korte, S. M., Koolhaas, J. M., Wingfield, J. C., & McEwen, B. S. (2005). The  
 12 Darwinian concept of stress: Benefits of allostasis and costs of allostatic  
 13 load and the trade-offs in health and disease. *Neuroscience and*  
 14 *Biobehavioral Reviews*, 29, 3–38.
- 15 Labrie, F., Luu-The, V., Labrie, C., & Simard, J. (2001). DHEA and its trans-  
 16 formation into androgens and estrogens in peripheral target tissues:  
 17 Intracrinology. *Frontiers in Neuroendocrinology*, 22, 185–212.
- 18 Leimar, O., Hammerstein, P., & Van Dooren, T. J. M. (2006). A new perspec-  
 19 tive on developmental plasticity and the principles of adaptive morph  
 20 determination. *The American Naturalist*, 167, 367–376.
- 21 Locke, J. L., & Bogin, B. (2006). Language and life history: A new perspective  
 22 on the development and evolution of human language. *Behavioral and*  
 23 *Brain Sciences*, 29, 259–280.
- 24 Marlowe, F. (2000). Paternal investment and the human mating system.  
 25 *Behavioural Processes*, 51, 45–61.
- 26 Marlowe, F. (2003). The mating system of foragers in the Standard Cross-  
 27 Cultural Sample. *Cross-Cultural Research*, 37, 282–306.
- 28 Marquez, C. J., & Rucas, S. L. (2008). *Sexual selection for neoteny: Are submis-*  
 29 *sive women more attractive?* Poster presented at the European Human  
 30 Behaviour and Evolution Conference. *Montpellier*, April 2–4, 2008.
- 31 McGlothlin, J. W., Jawor, J. M., & Ketterson, E. D. (2007). Natural variation  
 32 in a testosterone-mediated trade-off between mating effort and parental  
 33 effort. *The American Naturalist*, 170, 864–875.
- 34 Mendle, J., Turkheimer, E., D’Onofrio, B. M., Lynch, S. K., Emery, R. E., Slutske,  
 35 W. S., & Martin, N. G. (2006). Family structure and age at menarche: A  
 36 children-of-twins approach. *Developmental Psychology*, 42, 533–542.
- 37 Mendle, J., Harden, K. P., Turkheimer, E., Van Hulle, C. A., D’Onofrio, B. M.,  
 38 Brooks-Gunn, J.,... Lahey, B. B. (in press). Associations between father  
 39 absence and age of first sexual intercourse. *Child Development*.
- 40 Miller, G. (2000). *The mating mind. How sexual choice shaped the evolution of*  
 41 *human nature*. London: Heinemann.

- 1 Pellegrini, A. D., & Archer, J. (2005). Sex differences in competitive and  
 2 aggressive behavior: a view from sexual selection theory. In B. J. Ellis, &  
 3 D. F. Bjorklund (Eds.), *Origins of the social mind: evolutionary psychology  
 4 and child development* (pp. 219–244). New York: Guilford.
- 5 Pennington, R., & Harpending, H. (1988). Fitness and fertility among  
 6 Kalahari!Kung. *American Journal of Physical Anthropology*, 77, 303–319.
- 7 Quinlan, R. J. (2003). Father absence, parental care, and female reproductive  
 8 development. *Evolution and Human Behavior*, 24, 376–390.
- 9 Quinlan, R. J. (2007). Human parental effort and environmental risk.  
 10 *Proceedings of the Royal Society of London B*, 274, 121–125.
- 11 Quinlan, R. J., & Quinlan, M. B. (2007). Evolutionary ecology of human pair-  
 12 bonds. Cross-cultural tests of alternative hypotheses. *Cross-Cultural  
 13 Research*, 41, 149–169.
- 14 Roff, D. A. (2002). Variation and life history evolution. In B. Hallgrímsson &  
 15 B. K. Hall (eds.), *Variation: A central concept in biology*. Amsterdam/New  
 16 York: Elsevier.
- 17 Rowe, D. C. (2000). Environmental and genetic influences on pubertal devel-  
 18 opment: Evolutionary life history traits? In J. L. Rodgers, D. C. Rowe, and  
 19 W. B. Miller, (eds.), *Genetic influences on human fertility and sexuality:  
 20 Recent empirical and theoretical findings*, pp. 147–168. Boston: Kluwer.
- 21 Schmitt, D. P. (2005). Sociosexuality from Argentina to Zimbabwe: A 48-  
 22 nation study of sex, culture, and strategies of human mating. *Behavioral  
 23 and Brain Sciences*, 28, 247–311.
- 24 Schmitt, D. P., Alcalay, L., Allensworth, M., Allik, J., Ault, L., Austers, I., et al.  
 25 (2003b). Are men universally more dismissing than women? Gender  
 26 differences in romantic attachment across 62 cultural regions. *Personal  
 27 Relationships*, 10, 307–331.
- 28 Simpson, J. A., & Belsky, J. (2008). Attachment theory within a modern  
 29 evolutionary framework. In P. R. Shaver and J. Cassidy (eds.), *Handbook  
 30 of attachment: Theory, research, and clinical applications* (2nd ed.).  
 31 New York: Guilford.
- 32 Smith, P. K. (2005). Play: types and functions in human development. In  
 33 B.J. Ellis, & D. F. Bjorklund, *Origins of the social mind: Evolutionary psy-  
 34 chology and child development* (pp. 271–291). New York: Guilford.
- 35 Sroufe, L. A., Bennett, C., Englund, M., Urban, J., & Shulman, S. (1993). The  
 36 significance of gender boundaries in preadolescence: contemporary cor-  
 37 relates and antecedents of boundary violation and maintenance. *Child  
 38 Development*, 64, 455–466.
- 39 Storey, A. E., Walsh, C. J., Quinton, R., & Wynne-Edwards, K. E. (2000).  
 40 Hormonal correlates of paternal responsiveness in new and expectant  
 41 fathers. *Evolution and Human Behavior*, 21, 79–95.

- 1 Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., &  
2 Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-  
3 and-befriend, not fight-or-flight. *Psychological Review*, *107*, 411–429.
- 4 Tither, J. M., & Ellis, B. J. (2008). Impact of fathers on daughters' age at  
5 menarche: A genetically- and environmentally-controlled sibling study.  
6 *Developmental Psychology*, *44*, 1409–1420.
- 7 Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell,  
8 (ed.), *Sexual selection and the descent of man 1871–1971*, pp. 136–179.  
9 Chicago, IL: Aldine.
- 10 West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*.  
11 New York: Oxford University Press.
- 12 Wilson, D. S., & Yoshimura, J. (1994) On the coexistence of specialists and  
13 generalists. *The American Naturalist*, *144*, 692–707.
- 14 Winking, J., Kaplan, H., Gurven, M., & Rucas, S. (2007). Why do men  
15 marry and why do they stray? *Proceedings of the Royal Society B*, *274*,  
16 1643–1649.
- 17 Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history  
18 trade-offs favour the evolution of animal personalities. *Nature*, *447*,  
19 581–585.