# A Turning Point for the Life History Approach to Individual Differences

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Preprint v.1 (May 2024)

To appear in: Kanazawa, S. (Ed.), *Genes, Environments, and Differential Susceptibility: Current Topics in Evolutionary Developmental Psychology.* Cambridge University Press.

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# Abstract

The life history approach to individual differences has become a major influence in evolutionary psychology, not least thanks to the contributions made by Jay Belsky and his collaborators over the last three decades. Today the approach is at a turning point, with a lively dialectic between proponents and critics and a menu of theoretical and empirical challenges to address. In this chapter, I follow up on previous work and continue to critically examine the concepts and assumptions of the "fast-slow paradigm" in evolutionary psychology. Specifically, I try to clarify some aspects of the interplay between the demographic and psychological levels of analysis; make an updated case for the centrality of the mating-parenting trade-off in the organization of life history-related traits; describe the constellations formed by those traits, and introduce the notion of multiple fast/slow profiles; and (re)consider the role of puberty timing in relation to human life history strategies. Preserving the value of the life history approach demands that we work to keep the foundations healthy—constantly revising our concepts and assumptions, in the spirit of Jay's remarkable scientific career.

*Keywords*: behavior genetics; individual differences; life history theory; mating; motivation; personality; puberty; sociosexuality.

The idea that individual differences in personality and behavior can be linked to variation in life history strategies has been around for more than three decades; in the shape of what I have labeled the *fast-slow paradigm* (Del Giudice, 2020), it has been a steady influence on research and theorizing in evolutionary psychology. The story has been told before (e.g., Black et al., 2017; Del Giudice, 2018; Nettle & Frankenhuis, 2019), and here there is no space to revisit it in detail. What is beyond dispute is that the 1991 paper that Jay Belsky wrote with Laurence Steinberg and Patricia Draper was a critical turning point in the development of the paradigm, and a powerful motivator for its widespread adoption.

Belsky and colleagues (1991) famously proposed a developmental sequence or "cascade" in which stress and adversity in the family context influence parenting behavior, which in turn shapes attachment styles, interpersonal orientations, and—crucially—somatic development in the form of accelerated vs. delayed puberty. In a version of the cascade that has become canonical, puberty timing *mediates* the impact of early experiences on a suite of traits—timing of sexual debut, couple stability, and parental investment—that implement alternative life history strategies geared toward early (vs. late) reproduction, offspring quantity (vs. quality), and investment in mating (vs. parenting).<sup>1</sup> Chisholm (1993, 1999) completed the picture by including individual differences in mating strategies (restricted vs. unrestricted sociosexuality) and time preference (present vs. future orientation). In the following decades, Jay and his many coauthors went on to test and refine the model in a series of papers that is way too long to cite in full.<sup>2</sup> I have contributed to this line of research on a number of occasions (e.g., Del Giudice, 2009), including some collaborations with Jay that I remember with fondness and gratitude (e.g., Del Giudice & Belsky, 2010, 2011).

As the life history approach to individual differences reached a peak of popularity in the 2010s, it was also coming under closer scrutiny. Critics from inside and outside the paradigm started to question the theoretical soundness of key predictions; their connection with biological models of life history evolution; the validity of psychometric measures of "life history strategy"; the empirical links among behavioral traits, physical maturation, and reproductive outcomes; and the causal role of the early environment. The debate found a home in a memorable special issue of *Evolution and Human Behavior* (see Frankenhuis & Nettle, 2020). In my contribution to that issue, I traced the logic of the fast-slow paradigm from the level of species to that of individuals, highlighted the theoretical and empirical complexities involved, and tried to address the most pressing critiques in a constructive way (Del Giudice, 2020). I surely didn't want the field to throw the baby out with the bathwater; but it also seemed the right time to reconsider some assumptions that had been taken for granted (e.g., about the centrality of puberty timing) and suggest conceptual innovations (e.g., an "extended model" of life history-related traits allowing for multiple behavioral pathways toward mating and parenting effort; more on this below).

<sup>&</sup>lt;sup>1</sup> One should note that Belsky et al. (1991) did not commit to this particular version of the model, and left the door open to the possibility of more complex developmental interactions (see also Belsky, 2007).

<sup>&</sup>lt;sup>2</sup> Sorry, Jay! But readers can see Belsky (2007, 2012, 2019) to get up to speed.

Today, I believe the life history approach is at another turning point. The debate has progressed since 2020, with the publication of some notable papers that—in different ways take a critical stance toward the classical fast-slow paradigm (e.g., Dinh et al., 2022; Dinh & Gangestad, 2024; Gutiérrez et al., 2022; Međedović, 2021; Richardson et al., 2023, 2024; Volk, 2023). Collectively, these papers illuminate key points of tension, but also some welcome opportunities for progress and conceptual clarification. What we need is a coherent, compelling update of the paradigm; in the rest of the chapter, I follow up on Del Giudice (2020) and continue to lay the groundwork for this renovation project.

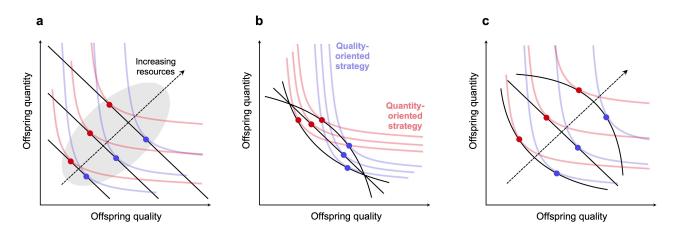
# **Clarifying the Interplay of Psychology and Demography**

While life history strategies can be described in demographic terms as schedules of reproduction and survival, the underlying allocations are instantiated by differences in physiology, morphology, and—most critically for animals with complex social lives—behavior (see Braendle et al., 2011; Del Giudice, 2020; Del Giudice et al., 2015). These life-history related traits yield stable individual patterns of prioritization among biological goals, which may be properly regarded as allocation *strategies* in a narrow sense and contrasted with *outcomes* such as fertility, longevity, reproductive timing, offspring quality, and other life history traits.<sup>3</sup>

Crucially, life history traits such as fertility and offspring quality are not a simple function of individual allocation strategies. At a minimum, they are the joint outcomes of allocation strategies, the amount of resources to be allocated, potentially other aspects of genetic/phenotypic quality, and (not least) chance. Hence, they may distort the underlying trade-offs and strategies, or even obscure them altogether. This point about quality and resources has been made any number of times (see e.g., Bolund, 2020; Del Giudice, 2020; Roff & Fairbairn, 2007), but it can be useful to illustrate it with a diagram (Figure 1).

As shown in Fig. 1a, quality-oriented strategists with more resources can easily invest *more* in offspring quantity than quantity-oriented strategists with less means. Both kinds of strategists invest more in quality *and* quantity as resources improve, albeit at different rates; thus, enough variation in resource availability can yield a positive correlation between quality and quantity in the population, even in presence of a trade-off between the two at the level of individual allocations. Fig. 1b shows that different strategies tend to diverge more when the trade-off becomes more severe (convex curve), but converge when it is relaxed (concave curve). Fig. 1c puts the two effects together under the assumption (which may or may not apply in any given real-life scenario) that the trade-off between offspring quality and quantity becomes more severe as resources get scarcer. Note that the two kinds of strategists in Fig. 1 are always following the same allocation rules—what changes are only the conditions they operate in.

<sup>&</sup>lt;sup>3</sup> Following Del Giudice (2020), I use "life history traits" to refer to the outcomes of life history allocations (e.g., age at first reproduction, fertility, longevity) and "life history-related traits" for the psychological, physiological, and morphological traits that mediate those allocations.



**Figure 1.** Schematic illustration of how different kinds of strategists make allocation decisions in presence of trade-offs and variation in resources. Black lines represent a trade-off between quality and quantity, at different levels of available resources. Light-colored lines are indifference curves for a quantity-oriented strategy (red) and a quality-oriented strategy (blue); red and blue dots indicate allocation decisions. Panel **(a)** shows how allocations change as resources increase or decrease. Note that, given a mixture of strategists and enough variation in resources, quality and quantity can be positively correlated in the population (grey ellipse) despite the trade-off at the individual level. In **(b)**, the strategies diverge more strongly when the trade-off becomes more severe (convex line) and converge when it is relaxed (concave line). In **(c)**, the trade-off becomes more severe when resources are scarcer, and milder when they are more abundant.

The problem is compounded by the highly stochastic nature of events such as reproduction and death, which injects noise into demographic life history traits. It is easy to underestimate the magnitude of this effect:<sup>4</sup> in studies of nonhuman animals, stochastic variation is often the dominant component of individual differences, typically accounting for more than 60% of the variance in longevity and fertility (e.g., Hartemink & Caswell, 2018; Snyder & Ellner, 2018). The bottom line is that, at the individual level, demographic life history traits are extremely noisy and cannot be expected to show large correlations with one another, let alone with environmental and behavioral predictors (for details see Del Giudice, 2020).

For all these reasons, psychological traits can reveal trade-offs and allocation rules more clearly than the life history traits that constitute their (noisy, context-dependent) outcomes. The two levels of analysis should neither be conflated nor pitted against each other, but connected within a coherent functional narrative that takes into account the relevant complexities and

<sup>&</sup>lt;sup>4</sup> A recent, high-profile example is a paper by Van de Walle et al. (2023) on individual variation in life history traits in mammals and birds. The authors subjected four traits to PCA within each species (age at first reproduction, lifespan, breeding frequency, and fertility); they regarded the first component as meaningful (and potentially representative of a FAST-SLOW continuum at the individual level) only if it explained more than 52% of the variance. But this requirement is virtually impossible to meet, considering that more of half of the variance of each trait is already likely to be just stochastic noise! (The problem was worsened by the very small sample size in some of the species.) Predictably, the first component approached the 52% threshold in only *one* species out of seventeen. Given the large amount of noise, one must also question whether the first components would actually capture the intended continuum dimension of variation (for details see the supplement in Del Giudice, 2020).

limitations. To facilitate this task and prevent common confusions, I will label demographic life history patterns as "FAST" and "SLOW" in all caps, and use lowercase "fast" and "slow" for allocation strategies and the constellations of life history-related traits (including psychological ones) that implement them in practice.

# **Demography and Psychology in Human Life Histories**

The correspondence, or lack thereof, between the psychological and demographic levels of analysis is a recurring theme in the literature on the fast-slow paradigm (see Black et al., 2017; Nettle & Frankenhuis, 2020). Contemporary human societies pose formidable challenges in this respect because accessible technologies for contraception and abortion have the potential to decouple mating and sex from reproduction. Thus, people who have more children (and start having them earlier) tend to be those with a strong *desire* to become parents, a disposition toward long-term commitments, and the willingness to invest the required time and effort. In contrast, those with less interest in children and a desire for multiple partners and uncommitted sex tend to postpone the decision to become parents and may end up having few offspring, if any.<sup>5</sup>

With this in mind, it is no surprise when "fast" traits such as unrestricted sociosexuality, larger numbers of sexual partners, and the like fail to correlate with reproductive outcomes—or even predict delayed reproduction and reduced fertility—in surveys from industrialized countries (e.g., Dinh et al., 2022; Gutiérrez et al., 2022; Međedović, 2021; see also Woodley of Menie et al., 2017). Clearly, one should not expect psychological traits and reproductive outcomes to align straightforwardly in presence of large-scale evolutionary mismatches (more discussion below).

But the problem is more general: for example, absent routine contraception or other social factors that amplify the quality-quantity trade-off, abundant resources can allow most people to start reproduction earlier and have comparatively more children, regardless of the underlying allocation strategies (e.g., <u>Figure 1</u>; see also the historical examples in Volk, 2023). However, early reproduction and high fertility do not, by themselves, constitute a FAST life history strategy. Across mammalian species (as well as birds), the full syndrome of FAST life histories is defined by elevated mortality (short lifespan) and reduced offspring quality in addition to early reproduction and high fertility (see Del Giudice, 2020, including the supplement). It would be a mistake to categorize demographic patterns as FAST or SLOW based on fertility and/or reproductive timing alone, because these terms refer to specific *combinations* of traits and not to the values of single traits (which can vary in a multitude of ways alongside FAST vs. SLOW).

This distinction is conceptually important: for example, energetic abundance can easily accelerate reproduction and increase fertility on a background of low mortality and high investment in offspring; calling this a FAST strategy may generate needless confusion (e.g., Volk, 2023). In contrast, country-level data across the world show a full-fledged FAST-SLOW continuum driven by differences in mortality. Specifically, elevated mortality predicts a

<sup>&</sup>lt;sup>5</sup> This pattern should emerge more clearly at higher education levels, tracking people's increasing effectiveness at using contraception and avoiding unwanted pregnancies (e.g., Peipert et al., 2011; Rottenstreich et al., 2017; Stifani et al., 2018). Low-education, "at risk" samples may tell a different side of the story.

combination of higher fertility, earlier age at marriage and first birth, and lower birth weight (Bulley & Pepper, 2017; Ellis et al., in preparation; Placek & Quinlan, 2012; Šaffa et al., 2019; Schmitt, 2005).<sup>6</sup> Mortality remains a robust predictor of fertility when the same population is followed over time, even controlling for economic factors (reviewed in Ellis et al., in preparation). Of course, cross-cultural and cross-species comparisons do not necessarily reflect the size and direction of associations at the individual level within a group, country, or species (see Del Giudice, 2020; Pollet et al., 2014), so one should be cautious about extrapolating from one level to another.

# The Centrality of the Mating-Parenting Trade-off

The remarkable intensity and duration of parental investment in our species—which is not limited to food and protection but includes teaching, social support, and in many cases the transmission of resources between generations—suggests that trade-offs between offspring quality (broadly conceived) and quantity should play an important role in human life history strategies and allocations. In turn, sustained parental investment is best promoted by stable, committed couple relationships, which are inherently in tension with the pursuit of other partners and/or sexual opportunities (see Szepsenwol & Simpson, this volume). The mating-parenting trade-off is relevant to both sexes but especially critical for men, who have a longer reproductive window than women, and can potentially sire many offspring with little or no investment (see Copping & Richardson, 2020; Del Giudice, 2018). Indeed, men's provisioning at times seems to double (at least in part) as a way to attract new mates; conversely, in women, additional mating effort is going to have diminishing returns on fertility (given the constraints imposed by pregnancy and lactation), but can succeed in attracting investment from multiple partners, especially if individual partners are unlikely to be committed and dependable (see e.g., Del Giudice, 2009). These are examples of how the sexes attempt to navigate the trade-off based on their specific cost/benefit balances.

# A Response to Dinh and Gangestad's Critique

In line with other theorists in this area (e.g., <u>Szepsenwol & Simpson, this volume</u>), I have proposed that the mating-parenting trade-off is a central aspect of human life history strategies, and the main organizer of the constellation of traits that make up the psychological fast-slow continuum (Del Giudice, 2018, 2020; more on this below). In a recent paper, Dinh and

<sup>&</sup>lt;sup>6</sup> The pattern becomes less clear if one looks specifically at countries in sub-Saharan Africa, which have experienced dramatic shifts in mortality in the space of a few decades, partly because of the HIV/AIDS epidemic (Anderson, 2010; Low et al., 2013). This is also an issue with Schmitt's (2005) finding that unrestricted sociosexuality was associated with higher life expectancy and lower fertility across countries (unweighted correlations .38\* and -.31), a pattern seemingly inconsistent with FAST life history strategies. However, inspection of the raw data (Schmitt, personal communication, April 25, 2024) reveals that these associations are almost entirely due to a cluster of four African countries (Botswana, Congo, Ethiopia, and Zimbabwe) with very low life expectancy, very high fertility, and low (restricted) levels of self-reported sociosexuality. These are the only sub-Saharan countries included in the study. Without those countries, the correlations are reduced to .10 for life expectancy and -.07 for fertility. Controlling for economic factors (GDP per capita) and the sex ratio (see Schmitt, 2005) yields partial correlations of -.10 with life expectancy and .40\* with fertility. This reanalysis is not conclusive by any stretch, but it highlights some of the complexities in the interpretation of cross-cultural data (se also Pollet et al., 2014).

Gangestad (2024) forcefully argued the contrary proposition—that the mating-parenting tradeoff is *not* a meaningful component of fast vs. slow strategies (which only concern allocations to current vs. future reproduction and offspring quality vs. quantity). Their critique is a valuable challenge to the received view in evolutionary psychology and a useful "stress test" of some common assumptions; but even if it raises some important issues, I find it unconvincing, and now briefly discuss why.

The argument advanced by Dinh and Gangestad rests on five main pieces of evidence and reasoning. First, comparative data from birds (Sibly et al., 2012) show that reproductive output<sup>7</sup> is higher in species with biparental care compared with female-only care.<sup>8</sup> However, the data plotted in the supplement (Fig. S2 in Sibly et al., 2012) suggest a more complex pattern, with high productivity when females alone (or males alone) care for *precocial* offspring—which, by definition, require comparatively little care—but not when offspring are altricial with long periods of dependency. The larger point is that patterns of offspring development and parental care should be considered jointly, not simply partialed out of one another as in Sibly et al. (2012). Another notable problem is that high output is *not* synonymous with a FAST life history strategy, as it only quantifies the organism's reproductive effort (excluding parental care) with no reference to mortality, longevity, or reproductive timing.

Second, Dinh and Gangestad analyze data from various species of primates, and find that monogamy is not systematically related to offspring production (also adjusted for body size) or to a weight-based index of quality vs. quantity. The main problem with this analysis is that monogamy in primates is not reliably linked to paternal care (Rosenbaum & Silk, 2022; Wright, 1990). For example, tarsiers (high in offspring productivity) are monogamous, but fathers do not care for infants; whereas callitrichids (also highly productive) have a flexible mating system that includes monogamy and show extensive paternal care (Dunbar, 1995; Wright, 1990). Among cercopithecines, which have promiscuous mating systems, several species can form stable pair bonds that support paternal investment (Rosenbaum & Silk, 2022; Städele et al. 2021). Chimpanzees also mate promiscuously, but some degree of paternal care occurs despite the lack of stable pair bonds (Murray et al., 2016). The disconnect between pair-bonding and paternal care across primate species means that, in general, monogamy is not a good proxy for investment in parenting over mating. Indeed, patterns of paternal care are so variable and functionally diverse in primates that one should not expect them to cluster strongly with other life history traits across species. But of course, the key question regarding human psychology is whether and how pair-bonding and paternal investment contribute to individual outcomes in our species, with its own ecology and behavioral mechanisms (Del Giudice, 2020).

This leads me back to Dinh and Gangestad's third source of evidence: a study by Marlowe (2001) showing that, across forager societies, a greater contribution to subsistence by men predicts higher fertility rates and shorter interbirth intervals, seemingly contradicting the notion that pair-bonding and paternal investment function to promote quality at the expense of

 $<sup>^7</sup>$  Measured as egg mass  $\times$  number of eggs per clutch  $\times$  number of successful clutches per year, adjusted for body mass.

<sup>&</sup>lt;sup>8</sup> Although the highest productivity is achieved by species with *male-only* care (Sibly et al., 2012).

quantity. But things are not that simple, because couple stability across forager societies peaks at *intermediate* levels of male contribution (i.e., when mothers and fathers need to cooperate and share the workload), and declines sharply when men contribute little to the diet, but also when they contribute most or all of the calories (Quinlan & Quinlan, 2007).<sup>9</sup> This indicates that the effect on fertility documented by Marlowe (2001) is not a function of stable, committed pair bonds and paternal investment, but of other ecological factors (such as the availability of alloparents). Other data from non-industrialized societies indicate that fathers' investments promote offspring quality more than quantity (e.g., Winking & Koster, 2015), and that paternal care declines systematically as pathogen risk increases, in line with the assumptions of the classical fast-slow paradigm (Quinlan, 2006; supplement in Martin et al., 2020).

Dinh and Gangestad then reason that, in women, unrestricted sociosexuality and multiple matings are unlikely to have evolved as components of fast strategies, as they do not substantially increase fertility and-particularly in ancestral environments-would have carried the risk of losing investment from the current partner, with cost for reproductive success.<sup>10</sup> The authors do not present data to this effect; they also pit committed pair bonds against concurrent or short-term sexual relationships, but ignore the very real possibility of serial monogamy with successive partners in the context of unstable pair bonds. In most forager societies, women can divorce and remarry; in fact, divorce is usually initiated by women and is especially common in early marriages, often granting women more freedom in choosing their next partner (Blurton Jones, 2016; Scelza, 2013). At least in some societies (e.g., the Pimbwe in Tanzania), the data show that multiple marriages increase women's fitness and reproductive success more than men's (Borgerhoff Mulder, 2009; Borgerhoff Mulder & Ross, 2019). These findings cast doubt on the idea that investing in mating effort and pursuing multiple partners cannot increase women's fertility, or that the expected outcome must be a net loss of paternal investment (as starkly exemplified by the Himba, whose men often provide food and gifts to the children they fathered outside of marriage; Scelza, 2013). That said, this issue remains understudied and poorly understood, and Dinh and Gangestad are absolutely right to put it in the spotlight.

The final piece of evidence in the argument is the lack of robust associations between pubertal timing and restricted vs. unrestricted sociosexuality in women (e.g., Batres & Perrett 2016; Dinh et al. 2022). The authors reason that, whereas puberty timing might contribute to determine life history trajectories, its small and inconsistent association with sociosexuality reinforces the idea that mating dispositions are not meaningfully related to the fast-slow continuum in humans. In a later section, I address the role of puberty timing in the detail it deserves. But there is also something to say about Dinh and Gangestad's narrow focus on sociosexuality as an indicator of mating effort, in isolation from other psychological constructs. This limits the value of their analysis, because allocation strategies are not determined by single life history-related traits, but depend on constellations of functionally connected traits that jointly reflect an individual's dispositions and priorities.

<sup>&</sup>lt;sup>9</sup> It is also of note that polygyny predicted higher marriage stability than monogamy; i.e., pair bonds can be stable and committed without necessarily being exclusive.

<sup>&</sup>lt;sup>10</sup> Dinh and Gangestad (2024) also discuss and (in my opinion correctly) discount the possibility of increasing the genetic diversity of one's offspring via multiple mating.

# **Constellations of Life History-Related Traits**

In previous publications (Del Giudice, 2018, 2020), I proposed a list of "core" psychological traits associated with fast-slow strategies. These are: impulsivity, present vs. future orientation, risk-taking, and sensation seeking; precocious vs. delayed onset of sexual desire and sexual debut; restricted vs. unrestricted sociosexuality; sensitivity to sexual/moral disgust; orientation toward long-term mating; stable vs. unstable romantic attachments (note that *stability* is not exactly the same as *security*; see Del Giudice, 2018); and exploitative vs. cooperative social attitudes.<sup>11</sup> Taken together, these traits paint a contrast between "risky, short term" and "safe, long term" psychologies, not just in the domains of mating and pair bonding, but also with respect to mutual interpersonal relationships and the weighting of potential dangers against rewards.

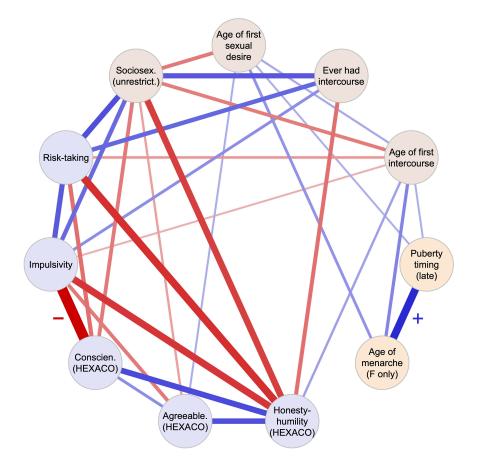
Broad-band personality traits such as conscientiousness, agreeableness, and honestyhumility also capture some of these dispositions; however, I believe the most meaningful level of analysis is that of individual differences in *motivation*, which represent the functional basis of psychometrically derived personality traits (Del Giudice, 2023a, 2023b; Denissen & Penke, 2008). Motivational profiles (i.e., differences in the salience of, sensitivity to, and responses to various kinds of threats and opportunities) are the flesh and blood of allocation strategies, and regulate the behaviors involved in mating, parental investment, self-protection, and so forth.<sup>12</sup>

The life history-related traits I listed above are linked to one another by a reliable pattern of correlations, exemplified by the data shown in <u>Figure 2</u>. In particular, earlier age of sexual debut is associated with impulsivity and sensation seeking, and is a robust predictor of unrestricted sociosexuality, higher numbers of sexual partners, and various kinds of risky behaviors (e.g., Hartman et al., 2018; Kwon et al., 2022; Međedović, 2021, 2022; Olesen et al., 2012; Richardson et al., 2023, 2024). Low agreeableness, conscientiousness, and honesty-humility also predict earlier sexual debut, more sexual partners, and higher chances of getting pregnant (e.g., Clark et al., 2021; Provenzano et al., 2018). Accordingly, antisocial behavior shows strong genetic correlations with early reproduction and increased fertility (Tielbeek et al., 2018); polygenic scores for earlier age at first birth predict more sexual partners, lower self-

<sup>&</sup>lt;sup>11</sup> Some researchers attempt to overcome the limitations of self-reports with objective laboratory tasks and games designed to measure impulsivity, cooperation, and so on (e.g., Copping et al., 2014a; Wu et al., 2017). Unfortunately, these tasks often suffer from poor reliability and questionable validity; for example, executive tests of inhibition also measure general intelligence (Friedman et al., 2008), and delay discounting tasks tend to mistake risk aversion for impulsivity (Lopez-Guzman et al., 2018). As a result, old-fashioned self-reports may predict outcomes much better than laboratory tasks, while the latter may fail to predict real-life behaviors almost completely (Creswell et al., 2019; Galizzi et al., 2018; Leeman et al., 2018; Venables et al., 2018; Voors et al., 2012). The bottom line is that, for all the problems of self-reports, laboratory tasks are far from "gold standards" and should be used and interpreted with caution.

<sup>&</sup>lt;sup>12</sup> The heterogeneous motivational content of broad-band personality traits (Del Giudice, 2023) also explains why extraversion and openness to experience (not included in the list) show contrasting relations with mating behaviors and other life history-related traits, depending on which specific facets one is considering (e.g., Holtzman & Strube, 2013; Manson, 2017). Likewise, measures of conscientiousness often include elements of performance (e.g., succeeding in being orderly and punctual) that are subject to self-evaluative distortions (perfectionism) and thus may not track motivation very closely (e.g., Mike et al., 2018; Mõttus et al., 2010).

control, and more externalizing behaviors (Richmond-Rakerd et al., 2020); and an "externalizing" factor largely defined by number of sexual partners, earlier sexual debut, and risk-taking (in addition to substance use and ADHD symptoms) is genetically correlated to impulsive, antisocial, and rule-breaking behaviors, and predicts higher numbers of pregnancies (Karlsson Linnér et al., 2021). Genetic correlations are particularly interesting because, to the extent that the traits and/or outcomes in question are linked by *horizontal* pleiotropy (i.e., the same genetic variants act independently on two traits; see Van Rheenen et al., 2019), they can reveal the underlying functional patterns in ways that are less confounded by environmental factors and modern mismatches.



**Figure 2.** Correlations among putative life history-related traits in a sample of 2,350 students from a Canadian university (64.8% females). Edges represent partial correlations (controlling for age, sex, and race/ethnicity), disattenuated for measurement unreliability (Cronbach's  $\alpha$ ). Only correlations with absolute values > .10 are shown; the largest correlation in the plot is -.90 between impulsivity and conscientiousness. Note that only 71.6% of the students had had sexual intercourse at the time of the study; hence, "age of first intercourse" and "ever had intercourse" should be considered together. Data: courtesy of Amanda Rotella. The code for the figure and a description of the variables are available at: https://doi.org/10.6084/m9.figshare.25729557

Researchers have also found genetic correlations between age at first intercourse, age at first birth, number of sexual partners, risk-taking, and fertility (Mills et al., 2021; Prince et al., 2022; see also Lawn et al., 2020; Barban et al., 2016). Mendelian randomization studies indicate that, at least in women, these correlations are partly due to *vertical* pleiotropy (i.e., genetic variants affect the first trait, which in turn has a causal effect on the second trait); specifically, earlier first intercourse predisposes women to have more sexual partners, an earlier first birth, more children, and engage in more risky behaviors (Lawn et al., 2020; Prince et al., 2022).<sup>13</sup>

Just like a single demographic feature such as early or late reproduction should not be confused with a full-fledged FAST or SLOW pattern, life-history related traits must be considered together to properly conceptualize fast vs. slow allocation strategies. Each of the traits I listed above is multi-determined by a variety of different influences (e.g., attractive men tend to have sex earlier, have more sexual partners, and develop less restricted sociosexual attitudes; see Arnocky et al., 2021; Copping et al., 2014b; James & Ellis, 2013), and can play multiple functional roles depending on context. This is especially true for broad-band personality traits like conscientiousness and honesty-humility, which are derived inductively from item correlations and not from the analysis of specific motivational mechanisms and tendencies.

The bigger question is: what is the best way to model the reciprocal relations among life history-related traits? Factor-analytic methods have important limitations, especially in view of the possible existence of multiple profiles within fast and slow strategies (see below). Unfortunately, I do not expect that network models based on the same traits and correlations (e.g., Manson & Kruger, 2022) will yield much additional insight. I believe that real breakthroughs in this direction can only come from an explicit model of human motivational mechanisms, including a functionally grounded map of their main working parameters and interrelations (I sketched a general architecture to facilitate this formidable task in Del Giudice, 2023a, 2023b). A functional model of how trait constellations arise would provide much better guidance about what to measure and how to measure it, and help overcome the shortcomings of psychometrically derived personality traits.

#### An Extended Model: Alternative Profiles within Fast and Slow Strategies

Before ending this section, I wish to briefly mention my proposal for extending the basic model of the psychological fast-slow continuum, a model that has been inherited (with successive modifications) from Belsky and colleagues' original theorizing (see Del Giudice, 2018).<sup>14</sup> The key insight is that, in our species, allocations to mating and parenting can be realized through a number of alternative pathways, which in turn should favor different combinations of cognitive and behavioral traits. For example, humans can transfer many kinds of resources to their offspring besides food and protection; particularly since the transition to agriculture, people can enhance the fitness of their children—and often their grandchildren—by

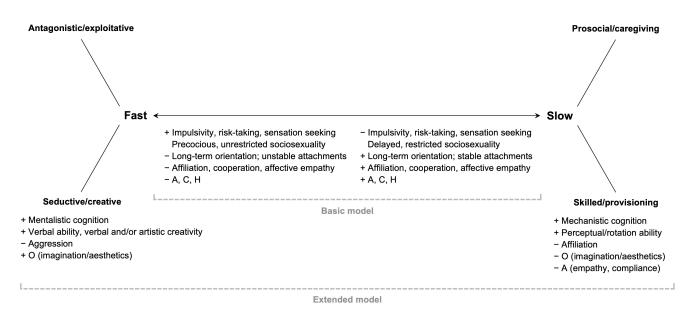
<sup>&</sup>lt;sup>13</sup> Note that these genetically informed studies include a proportion of older people who had their sexual debut before contraception became easily available. This probably contributes to strengthen the correlations of various traits with the age at first birth and the number of children, in ways that are more revealing of past conditions but less generalizable to present ones (Prince et al., 2022).

<sup>&</sup>lt;sup>14</sup> The following paragraphs are adapted from Del Giudice (2018) and the supplement in Del Giudice (2020).

endowing them with land, cattle, money, and other forms of wealth (Borgerhoff Mulder et al., 2019; Jones, 2015). This opens up an alternative pathway to parental effort: especially for men, investment in parenting may involve the accumulation and transmission of wealth in addition to (or in place of) direct caregiving and provisioning.

Another pivotal innovation in our species is the evolution of dual status hierarchies based on *dominance* and *prestige* (Henrich & Gil-White, 2001). The relevant point is that status and influence can be gained not only with the threat of physical force, but also with the possession of valued skills and knowledge. This multiplies the pathways to mating success—particularly for men, who benefit more consistently from status and wealth (e.g., Nettle & Pollet, 2008; von Rueden & Jaeggi, 2016). The material benefits of status can also be transferred to one's family and offspring and thus channeled into *indirect* parenting effort.

Because the mating-parenting trade-off in humans can take a variety of forms, the fastslow continuum is unlikely to be associated with a unitary set of traits; instead, I proposed that fast and slow strategies comprise a range of "profiles," with similar implications for basic tradeoffs but distinct psychological mediators (Figure 3).



**Figure 3.** An extended model of life history-related traits in humans (reproduced with permission from Del Giudice, 2018). The basic model only distinguishes between fast and slow strategies; the extended model postulates the existence of alternative profiles defined by specific clusters of psychological traits. A = agreeableness; C = conscientiousness; H = honesty-humility; O = openness to experience.

In the basic model, fast strategies are associated with antagonistic, exploitative behaviors and overt dominance competition (particularly in males). However, an alternative way to channel mating effort is to invest in prestige competition and courtship through a combination of verbal skills, mentalizing, and creativity. The corresponding profiles can be labeled *antagonistic/exploitative* and *seductive/creative*. These profiles define separable regions in the psychological space of fast strategies, and are associated with predispositions for different kinds of mental disorders (e.g., psychopathic/antisocial personalities vs. narcissism and positive schizotypy).

On the slow side of the continuum, the basic model focuses on traits that favor direct parental investment, such as affiliation, high agreeableness, and affective empathy. These traits imply a warm, nurturing attitude and describe the *prosocial/caregiving* psychological profile. However, direct caregiving is not the only route to successful parental investment. Especially for men, another option is to contribute mainly with status and resources—both of which can be acquired through mastery of technical skills, broadly defined. This male-typical pattern (which has likely become more common in the recent evolutionary past, after the transition to agriculture) creates a niche for what I have labeled a *skilled/provisioning* profile—characterized by lower affiliation and empathy, enhanced mechanistic and visuospatial skills at the expense of imagination, and increased risk for disorders in the autism spectrum.

The taxonomy I just outlined is based on a broad array of evidence (see Del Giudice, 2018; Del Giudice & Haltigan, 2023), but also still speculative and preliminary in many respects. The point I want to stress is that, while the classical model of fast vs. slow strategies captures something important about human variation (Figure 2), it is too simple and one-dimensional for the complexities of our mating and social psychology. As a result, it can miss—or potentially misinterpret—some important, distinctly human patterns of individual differences. The extended model summarized in Figure 3 is an attempt to broaden the scope of the paradigm and make it more flexible and realistic, without losing the (heuristically valuable) parsimony of its basic assumptions.

# The Role of Puberty Timing

A question has been left hanging throughout this chapter: what about puberty timing? Ever since Belsky and colleagues (1991) made their "uncanny prediction", this issue has attracted controversy and motivated a great deal of research and theorizing (see Belsky, 2012, 2019, 2024; Belsky et al., 2012; Colich et al., 2020; Ellis, 2004; Ellis et al., in preparation; Glass et al., 2022; James & Ellis, 2013). Puberty timing figures prominently in the recent critiques by Volk (2023) and Dinh and Gangestad (2024), and is the main focus of Richardson et al.'s (2023, 2024) genetic analyses. The topics under debate include the respective roles of energy availability and psychosocial stress in determining the timing of maturation; the weight of genetic vs. environmental factors; and the plausibility of a meaningful causal influence of the family context (a crucial aspect of Belsky et al.'s model), in view of the substantial heritability of puberty and the apparent lack of *shared* environmental effects in genetic studies (see Del Giudice, 2020).

Clearly, the conversation around the function and mechanisms of puberty timing is not going to end anytime soon. There is still legitimate uncertainty about important ancillary issues, such as the existence and size of non-additive genetic effects, which could inflate heritability estimates and deflate the apparent contribution of the shared environment (Ellis, 2004; for a selection of contrasting findings see Anderson et al., 2007; Hur et al., 2019; Kirk et al., 2001; Towne et al., 2005; Zaitlen et al., 2013). The contention that life history strategies (including the

timing of menarche in girls) are fundamentally driven by energetics, with no meaningful role for psychosocial stress before modernization (Volk, 2023), has been energetically countered by Ellis and colleagues (in preparation). I side with Ellis et al. on the notion that energetic scarcity and cues to extrinsic mortality can have countervailing effects on life history traits, so that mortality cues tend to entrain FAST strategies, while energetic stress tends to delay reproduction and constrain the fertility rate (not the same as a SLOW pattern if mortality is high and parental investment remains limited). However, the evidence on psychosocial stress and menarche is still not conclusive in either direction, especially considering the plausibility of genetic confounding (se Richardson et al., 2024) and the many differences between ancestral and modern environments.

### **Puberty Timing and the Fast-Slow Continuum**

While the intricate debates on puberty timing remain extremely interesting in their own respect, I have come to the conclusion that they are not as crucial to the fast-slow paradigm as many researchers assume. In fact, the Gordian knot can be cut by recognizing that Belsky and colleagues (1991) overestimated the importance of puberty as a node in the development of life history strategies (see also Del Giudice, 2020). From a theoretical perspective, a common (if often implicit) mistake is to view the timing of sexual maturity as a "pure" mediator of the tradeoff between current and future reproduction-a role that, in formal models and animal studies, is usually played by the age at first reproduction. But this is not the case: because puberty also brings about the intensification and then cessation of physical growth, it is best understood as the confluence of multiple trade-offs-not just about the onset of reproduction but also about the allocation of energy to different kinds of somatic effort, most notably body growth versus body maintenance (immune function, tissue repair, etc.). This trade-off can complicate the costs and benefits of early puberty, not only when resources are scarce but also when the risk of infection is elevated (Reiches, 2019; see also Zhang et al., 2018). And since height contributes to formidability and attractiveness in men, anticipating puberty in conditions of energetic stress (thus growing a smaller body) can be detrimental to fast, mating-oriented males.

For all these reasons, the expectation that puberty timing should align neatly with the fast-slow continuum must be reconsidered. More generally, our species has a long reproductive window, remarkable flexibility in the timing of reproduction, and an extended period of care and provision for dependent offspring. These factors converge to reduce the importance of the exact timing of sexual maturation—particularly for men, who are not limited by the physiological constraints of pregnancy, lactation, and menopause, and whose reproductive prospects depend more critically on the age of their partners than on their own (e.g., Borgerhoff Mulder & Ross, 2019).

Empirically, puberty timing does not enjoy a central place in the constellation of life history-related traits and outcomes. In industrialized countries, earlier puberty has a causal effect on the timing of sexual debut (with correlations around .10-.20) and on the age at first birth in women, but otherwise is mostly unrelated to fertility, sociosexuality, and the number of sexual partners (Baams et al., 2015; Barban et al., 2016; Batres & Perrett 2016; Belsky et al., 2010; Dinh et al., 2022; Lawn et al., 2020; Magnus et al., 2020; Prince et al., 2022; Richardson et al., 2023, 2024; Tielbeek et al., 2018). This pattern is clearly reflected in the data of Figure 2. In

large studies, one can detect small associations between earlier puberty and risky/antisocial behaviors, but they do not seem to be causal—meaning that puberty and risk-taking covary because they share common influences, not because puberty timing affects risk-taking (Padrutt et al., 2023; see also Prati & Tomasetto, 2022).

In non-industrialized and/or non-Western societies, the onset of menarche can play a more significant role because it is often tied to a girl's readiness for marriage and childbearing (with some extreme cases in which girls get routinely married shortly after menarche). In a crosscultural dataset of foragers and farmers, Hochberg and colleagues (2011) found a correlation of .76 between the average age at menarche and at first reproduction; the correlation between age at menarche and fertility rate was -.21. However, it is important to remember that these are correlations at the level of group averages; at the level of individuals within a group, both individual differences and stochasticity kick in, and the associations may change substantially. In a review of studies from low- and middle-income countries, Ibitoye and colleagues (2017) found a consistent effect of the age at menarche on the age at marriage and first birth; within-country correlations at the individual level were in the .15-.30 range,<sup>15</sup> similar to other studies not included in that review (e.g., Pascual et al., 2005). These correlations are meaningful, even if not extremely large. In a study of Kipsigis farmers, Borgerhoff Mulder (1989) found negative correlations between age at menarche and fertility, likely due to the shared effects of nutrition on both maturation and fertility (i.e., not because earlier menarche increases fertility to a substantial degree).<sup>16</sup> These findings lend support to the idea that, in ancestral environments, puberty timing in girls contributed to regulate the onset of reproduction in response to varying energetic conditions, and possibly other environmental cues (see also Ellis et al., in preparation; again, note that early reproduction alone does not automatically equate to a FAST life history strategy).

Lastly, I want to briefly address is the possibility that girls who mature earlier suffer from higher mortality risk when they grow up (Charalampopoulos et al., 2014). Dinh and Gangestad (2024) called attention to this finding, as a potential clue to the functional connection between puberty timing and fast vs. slow strategies. As it turns out, most of the newer studies and meta-analyses show U- or J-shaped effects of age at menarche on cardiovascular risk, cardiovascular mortality, and all-cause mortality—meaning that risk is elevated both in early-maturing *and* latematuring girls compared with those in the middle (Behboudi-Gandevan et al., 2024; Liang et al., 2021; Lozano-Esparza et al., 2021; Yan et al., 2024; Yang et al., 2017). The same U-shaped pattern emerges when mortality risk is predicted with genetic scores for early vs. late age at menarche, instead of the actual age (Liang et al., 2021). Mendelian randomization studies have found causal associations between early puberty in males and shorter lifespan (Hollis et al.,

<sup>&</sup>lt;sup>15</sup> Many of the studies reviewed by Ibitoye et al. (2017) omit to report correlations, but they usually tabulate averages for different bins of the distribution of age at menarche. In most cases, a one-year change in age at menarche corresponds to a change of 0.5 to 1 years in age at marriage and/or first birth. Assuming that the standard deviation of the age at marriage or first birth is roughly 3 times larger than that of menarche (see Goodman et al., 1985; Pascual et al., 2005; Raj et al., 2015), the corresponding correlations range between .17 and .33. This back-of-the-envelope calculation matches the actual correlations and regression coefficients reported in some of the studies in the review, which range between .16 and .30.

<sup>&</sup>lt;sup>16</sup> The correlations were -.22 with fertility rate (N = 80; 95% CI [-.42, .00]) and -.53 with lifetime reproductive success (N = 33; 95% CI [-.74, -.22]). Confidence intervals are very wide, so one should take these effect sizes with a grain of salt.

2020), and between early menarche and cardiovascular risk (with BMI as a partial mediator; Ardissino et al., 2023; Magnus et al., 2020). However, none of these studies tested for nonlinear, U-shaped effects of genetic scores, so the possibility remains open.

The disorders associated with the timing of menarche are "diseases of modernity" such as diabetes, cancer, hypertension, and cardiovascular disease (Corbett et al., 2018); moreover, the specific risk profiles differ between early and late maturers (e.g., SadrAzar et al., 2023). For this reason, it is hard to estimate the impact of menarche timing on health and survival in ancestral environments, or determine whether early or late maturation was likely to be more costly for survival. At the moment, this remains an intriguing topic whose evolutionary implications are still far from clear.

#### The Case of Sexual Debut

In contrast with puberty *per se*, the evidence consistently indicates that the timing of sexual debut—which reflects the convergence of physical maturation and the awakening of sexual motivations—works as an important node in the development of fast vs. slow life strategies. Earlier onset of sexual behavior correlates with unrestricted sociosexuality and consistently predicts more sexual partners, higher risk-taking, earlier age at first reproduction, and (at least in some studies) higher fertility; as I noted earlier, these associations appear to involve a causal effect of sexual debut on other traits (Barban et al., 2016; Karlsson Linnér et al., 2021; Lawn et al., 2020; Međedović, 2021, 2022; Mills et al., 2021; Olesen et al., 2012; Prince et al., 2022; Richardson et al., 2023, 2024; see Figure 2).

In view of the long-standing debate about the genetic and environmental determinants of puberty, it is especially noteworthy that the timing of sexual debut shows a marked influence of shared environmental factors. In twin studies, the shared environmental component accounts for 20-40% of the variance—about as much as the genetic component (Carlson et al., 2014; Richardson et al., 2023, 2024; Waldron et al., 2007).<sup>17</sup> If one is looking for a developmental marker of fast vs. slow strategies—one that is firmly embedded in a constellation of functionally related traits, capable of influencing life history-related outcomes and behaviors, and responsive to the family environment—sexual debut is clearly a better candidate than puberty. Granted, the notion that early experience influences the onset of sexual behavior is not as unique or "uncanny", but it may prove just as scientifically fertile. Of course, no single trait can stand in for a whole, emergent allocation strategy; just like other life history-related traits, the timing of sexual debut is multi-determined by a variety of factors that include a person's attractiveness, the intensity of parental and social control, and so forth. Also, the associations of sexual debut with other traits should be investigated more thoroughly in non-Western and non-industrialized settings (see for example the mixed findings by Richardson et al., 2020).

<sup>&</sup>lt;sup>17</sup> The age at first reproduction also shows significant shared environmental effects, in the 10-20% range. The smaller value might be due to the higher individual stochasticity of reproduction compared with sexual intercourse; this is consistent with the fact that the nonshared environment (which also captures randomness and various kinds of noise) accounts for more than half the variance in the age at first birth, but not in the age at sexual debut (Kirk et al., 2001; Tropf et al., 2015). Note that proportions of variance inflate the apparent differences between smaller and larger effects; for example, if the shared and nonshared environments account for 20% and 60% of the variance (respectively), the impact of shared factors on the real-world scale of the phenotype is not one third, but  $\sqrt{1/3}$  or about 58% as large as that of nonshared factors (for details see Del Giudice, 2021).

# Conclusion

Throughout his impressive career, Jay has never stopped moving forward—every time we get to chat, he's been thinking about a new piece of evidence, reconsidering an old idea, toying with some interesting hypothesis, and—not rarely—changing his mind. As I was finishing this chapter, I learned that he has just written a new book on the "nature of nurture" (Belsky, in press), in which he grapples with the really big question of how to *think* properly about human development and reconcile perspectives and findings that, on the surface, seem to contradict one another.

I dedicate this chapter to the spirit of conceptual integration and constant revision that animates Jay's work—and, I hope, some of my own work as well. The life history approach that owes so much to that 1991 paper has a lot of value in it, but preserving this value demands that we work to keep the foundations healthy. Looking at the future, I see three possible scenarios. First, some researchers may abandon the fast-slow paradigm altogether, based on what I see as occasionally insightful but overwrought critiques (e.g., Sear, 2020; Zietsch & Sidari, 2020). Second, they may follow the path traced by Dinh and Gangestad (2024), and focus on a demographic FAST-SLOW continuum decoupled from the regulation of mating and parenting. In the scenario that I favor (spoiler alert!), classical ideas about fast vs. slow strategies are refined, tested, and functionally connected to demographic patterns, keeping the focus on the psychological level of analysis and particularly on the mechanisms of motivation. The conversation around these issues has never been more interesting, and—whatever the outcome our discipline will be richer and stronger because of it.

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