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Environmental Risks, Life-History Strategy, and Developmental Psychology

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Abstract

In recent decades, life history theory (LHT) has provided an important theoretical framework for understanding human individual differences and their developmental processes. The conceptual complexity and multidisciplinary connections involved in the LH research, however, might appear daunting to psychologists whose research might otherwise benefit from the LH perspective. The main purpose of this review, therefore, is to introduce the evolutionary biological backgrounds and basic principles of LHT as well as their applications in developmental psychology. This review is organized into five parts, starting with an overview of key concepts in LHT, which clarifies the relationship among LH strategy, LH-related traits, and the fast-slow paradigm of LH variation. We proceed to review theoretical and empirical work related to four basic LH trade-offs, summarized by an integrated descriptive model of LH trade-offs that shape different LH strategies in humans. We then explain the effects of four aspects of environmental risks (morbidity-mortality threats, competition, resource scarcity, and unpredictability) on human LH strategy. This is followed by a discussion of LH calibration models in evolutionary developmental psychology that explicates the environmentally sensitive developmental processes that contribute to variation and plasticity in LH-related traits and ultimately human LH strategies. Finally, we highlight a few outstanding questions and future directions for LH research in psychology and conclude with why we think it is important that developmental psychology should embrace the LH approach.

Keywords: life history theory, life-history trade-off, environmental harshness, environmental unpredictability, evolutionary psychology, developmental psychology

An implicit fact of the evolution of life is that organisms have only limited energy “budget” to spend on any life function (e.g., growth, maintenance, mating, and parenting), resulting in trade-offs among competing demands among these life functions (Del Giudice et al., 2015; Hill & Kaplan, 1999). Building on this premise, life history theory (LHT) is an evolutionary biological theoretical framework that explains how organisms allocate their energy to various fitness-enhancing activities in their life cycle (Del Giudice et al., 2015; Ellis & Del Giudice, 2019). It is assumed that natural selection should favor the optimal combination of life-history (LH) traits (e.g., lifespan, fertility rate, interbirth interval, offspring size) that, on average, lead to the greatest inclusive fitness in a certain environmental condition (Del Giudice et al., 2015; Ellis et al., 2009; Stearns, 1992). The bioenergetic resource allocation to a certain life function constitutes an organism’s LH strategy (Chang, 2018; Del Giudice et al., 2015; Ellis et al., 2009). A given species has its specific LH strategies concerning, for example, growth speed, age at first reproduction, offspring quantity, and parental investment (Stearns, 1992), which may also vary within species and show developmental plasticity (i.e., the ability of organisms to react to internal or external inputs through development; West-Eberhard, 2003).

LHT has profound ramifications beyond patterns of biological reproduction. The LHT framework is increasingly adopted in developmental psychology as a unifying explanation of developmental processes, developmental outcomes, and the roles of resource and environmental risks (Chang, 2018; Del Giudice et al., 2015; Ellis & Del Giudice, 2019). However, this burgeoning research field faces many challenges due to the cross-discipline gaps. Conceptual ambiguities, methodological issues, and oversimplified or inaccurate assumptions detached from their biological foundations in LH-inspired psychological research have been put under scrutiny in recent years (e.g., Copping et al., 2014; Richardson et al., 2017; Stearns & Rodrigues, 2020; Zietsch & Sidari, 2020).

Of course, none of these challenges should discourage researchers from using the LHT framework to understand patterns of individual difference and developmental calibration of behavioral and psychological traits. The current review aims to facilitate such goals by providing

an up-to-date summary of the main theoretical issues of LHT and clarifying some of the conceptual ambiguities from the perspective of human research. We begin with a bird's-eye view of different theoretical models and key concepts comprising the LHT framework. This is followed by a review of the conceptual issues and empirical evidence related to four basic LH trade-offs, how they are affected by four different aspects of environmental risks, and the LH calibration models of developmental processes that give rise to LH-related traits underlying different LH strategies. The last section presents a few outstanding conceptual and empirical issues about the application of LHT to developmental psychology, and potential future directions.

Key Concepts in LHT

The initial LHT framework is built on MacArthur and Wilson's (1967) r/K model, which focuses on population density (reflecting intraspecific competition) as the driving force of variations in LH strategy. At a lower population density, LH traits evolve to maximize the rate of population growth (r selection). Whereas, at a higher population density, LH traits evolve to maximize competitiveness in the population near the carrying capacity of the environment (K selection). Pianka (1970) extended this framework and extrapolated that the evolution of LH traits should converge on various evolutionary equilibria that form an r-K continuum.

An alternative explanation of LH variation highlights age-specific mortality and its variability as reasons behind the evolution and development of LH strategies that vary on a *fast-slow continuum* (Ellis et al., 2009; Healy et al., 2019; Michod, 1979). In general, organisms with higher juvenile mortality are expected to mature and start reproduction earlier (Berrigan & Koella, 1994), which allows organisms to convert somatic resources into reproductive output as quickly as possible (a fast strategy). Organisms with high overall mortality or adult-specific mortality are expected to grow faster, have higher fertility, and live a shorter lifespan, rather than to invest heavily in somatic resources, which would be lost when the organism is hit by mortality. The opposite pattern would prevail in low-mortality species (including humans), which allow more energy and time to be invested in embodied capital that enhances

competitiveness (a slow strategy; Ellis et al., 2009; Mace, 2000; Promislow & Harvey, 1990). It is theorized that the variability or unpredictability of mortality should have a similar impact on LH evolution as the mean level of mortality (Stearns, 1992).

The r-K and fast-slow accounts of LH variations are by no means mutually exclusive, as population density and age-specific mortality might both contribute to the selection of LH strategies at the *between-species* or *between-population* level. Recent density-dependent models have sought to mold together these two selective pressures by asserting that they operate at various stages of population fluctuation (Lande et al., 2017; Wright et al., 2019). For example, one mathematical model showed that the magnitude of environmental stochasticity might be responsible for the classic r-K trade-off, with r-selection prevailing in environments with high variability of mortality and K-selection prevailing in environments with low variability (Lande et al., 2017). Importantly, some theoretical models that incorporate density-dependent factors also draw predictions in accordance with a fast-slow continuum (Wright et al., 2019). The descriptive model by Ellis et al. (2009) integrated the effects of morbidity-mortality (i.e., external causes of death or disability; the inclusion of “morbidity” allows this term to encompass partial loss of fitness) with density-dependent factors such as resource scarcity and intraspecific competition. It is postulated that adults experiencing low morbidity-mortality in high-density populations would manifest slow LH traits, whereas adults experiencing high morbidity-mortality (not due to resource scarcity) or low morbidity-mortality in low-density populations would show fast LH traits (Ellis et al., 2009). Re-examining existing cross-species data, Del Giudice (2020) found that the main axis based on the fast-slow continuum typically accounts for 70-80% of the variance in biological LH traits (30-50% after controlling for body size).

Researchers also seek to use intuitive and concise ways, most notably the “fast-slow paradigm” (Del Giudice, 2020; Sear, 2020), to describe the coordinated patterns of the covariance of LH-related traits underlying *within-species* LH variations (Del Giudice et al., 2015; Figueredo et al., 2006). Del Giudice (2020) posits that LH-related traits are (a) represented by stable individual differences, (b) linked to allocations in LH trade-offs, and (c) mediators of

those allocation processes. In other words, LH-related traits (distinguished from the basic LH traits such as age at maturity, age-specific fertility, age-specific survivability; Roff, 2002) affect LH strategy through regulating “non-refundable” bioenergetic investment (including energy and time) in a certain domain of life function (e.g., reproductive efforts and somatic efforts). Individual differences generated by LH-related traits represent developmental plasticity (West-Eberhard, 2003), which involves durable structural or functional changes to biological systems through developmental processes.

Behavioral and cognitive traits such as early sexuality, increased mating efforts, impulsivity, and lower performance of deliberate mental abilities (e.g., executive functions) are believed to contribute to fast LH strategies, whereas the opposite behavioral and cognitive traits are believed to underlie slow LH strategies (e.g., Copping et al., 2013; Del Giudice et al., 2015; Figueredo et al., 2006; Kruger, 2017; Ugglå & Mace, 2015; Figueredo et al., 2012). However, not all LH-related traits can be placed on a single fast-slow axis (Del Giudice, 2020; to be discussed in greater detail below). An over-reliance on the fast-slow continuum may overlook the complex relationships among different basic LH trade-offs, and the evolutionary and genetic basis for the fast-slow paradigm is still poorly understood and sometimes controversial (Del Giudice, 2020; Zietsch & Sidari, 2020).

Basic LH Trade-offs and Human LH Strategy

A central tenet of LHT is that organisms’ allocation of limited bioenergetic capitals during their lifespan leads to trade-offs among a variety of life functions (Del Giudice et al., 2015; Stearns, 1992). Natural selection should operate on the phenotypes of these LH trade-offs that eventually produce adaptive combinations of LH traits. However, “adaptive” does not mean costless (Ellis & Del Giudice, 2019). For instance, the high mating frequency may produce more surviving offspring (which allows it to outcompete the alternative strategy of low mating frequency) but also incur health risks (e.g., potential exposure to sexually transmitted pathogens) that might undermine future reproductive opportunities (Del Giudice et al., 2015). LH trade-offs occur between different fitness components, which can be categorized into somatic effort (e.g.,

growth, development, and maintenance) and reproductive effort (e.g., mating, parenting, nepotism; Geary, 2002). Four basic LH trade-offs are frequently highlighted in the literature: maintenance versus growth, current reproduction versus future reproduction, offspring quantity versus offspring quality, and mating efforts versus parenting efforts (Del Giudice et al., 2015; Ellis et al., 2009).

Growth Versus Maintenance

In order to survive and reproduce, organisms must allocate a minimal amount of energy to maintenance and growth (Bogin et al., 2007). Maintenance involves brain metabolism, DNA repair, immune function, and behavioral defense against predators. Growth involves allocating energy to the development of the physical body (including genitals) and, in some animals including humans, social and cognitive functions. In other words, growth investment encompasses investment in growth quality (e.g., investment in larger body size), which facilitates energy production or energy use efficiency in animals (van Noordwijk & de Jong, 1986), and investment in growth speed (e.g., investment in sexual maturity), which facilitates earlier reproduction.

The trade-off between growth and maintenance occurs mainly from prenatal to juvenile periods (Bogin et al., 2007). This is demonstrated by research on physical growth and health in humans. On the one hand, early puberty timing (indicating fast growth) is associated with poor mental and physical health (indicating low maintenance) in diverse populations (Day et al., 2015; Ellis, 2004; Ellis & Del Giudice, 2019). On the other hand, there is also evidence that higher immune activation (increased allocation to maintenance) during childhood predicts slower gains in height (decreased allocation to growth), and the effect was greater when the diversion of energy to immunity occurred earlier and for those with low energy reserve (i.e., low body fat; McDade et al., 2008).

Current Versus Future Reproduction

Once organisms reach sexual maturity, they face the additional trade-off between immediately converting available bioenergetic resources to current reproductive success (e.g.,

mating efforts, childbirths, or parenting efforts) and continuing somatic investment that would contribute to future reproductive success. This trade-off between current and future reproduction is most directly reflected in the effects of reproductive timing. Research on Ache hunter-gathering communities, for example, found that delayed reproduction is associated with a longer growth period that implies greater likelihood of not surviving to first reproduction and bigger adult body size, which, in turn, is associated with higher future fertility (Hill & Hurtado, 1996). By contrast, other research showed that earlier age at first childbirth predicted worse health status, stunted growth, and poorer nutritional status in adolescent girls (Mell et al., 2018; Rah et al., 2008).

The trade-off between current and future reproduction might have selected for physiological mechanisms and behavioral plasticity that safeguard maternal survival (and thus future reproductive opportunities and the survival of existing offspring) against non-optimal reproductive timing. Research has found adjustments of female reproductive endocrinology (e.g., depressed estradiol and progesterone levels in the ovary) that function to curtail conception and childbirth under undernutrition, elevated workload, and psychological stress (Vitzthum, 2009). In comparison, men's investment in current reproduction is much less constrained by short-term energetic conditions due to inexpensive gamete production. Men's reproductive behaviors are modulated by testosterone production, which is affected by age and longer-lasting energetic conditions (Ellison, 2003). Further, research showed that men's and women's preferences for early versus late reproductive timing were sensitive to contexts and childhood socioeconomic status (SES; Griskevicius et al., 2011a). Qualitative studies in various cultures found that women also engage in conscious evaluation of the pros and cons associated with early and late motherhood (reviewed by Nettle, 2011).

Quantity Versus Quality of Offspring

According to the classic r/K model, the r strategy of giving birth to a large number of low-quality offspring trades off with the K strategy of rearing a small number of high-quality offspring (MacArthur & Wilson, 1967). This quantity-versus-quality trade-off is based on the

fact that parents only have finite resources to allocate to parental investment, which leads to the corollary that each additional offspring necessarily reduces the average investment per offspring. This trade-off not only affects parents' reproductive success but also has multigenerational effects on the survival, embodied capital, and reproductive success of future generations (Hill & Kaplan, 1999; Lawson & Borgerhoff Mulder, 2016). On the one hand, the "quantity" strategy may produce more surviving offspring in environments with sufficient resources and low competition, but leave very few surviving offspring in environments with intense resource competition (Wright et al., 2019). On the other hand, the "quality" investment in the forms of parental care, provisioning, protection, and education (all of which enhance offspring quality) may lead to more surviving children and grandchildren in densely populated, competitive environments (Ellis et al., 2009).

A considerable amount of anthropological research (e.g., Borgerhoff Mulder, 2000; Hagen et al., 2006; Hill & Hurtado, 1996; Walker et al., 2008) examined the trade-off between offspring quantity (indicated by fertility or sibship size in demographic survey data) and quality. The latter can be measured in terms of survivability (growth quality) or socioeconomic success. To begin, there are robust findings indicating that offspring quantity trades off with offspring quality in terms of survivability. Lawson et al. (2012), for instance, examined data across 27 sub-Saharan African countries and found that fertility is negatively associated with offspring survival, although mainly due to sibling competition for resources. Similarly, having more siblings is associated with increased risks of malnutrition (e.g., stunting, underweight, and wasting) in diverse populations (Sengupta et al., 2010; Victora et al., 1986). There is also robust evidence that the size of sibship is associated with socioeconomic indicators of offspring quality, such as lower school performance, educational attainment, and adult income (Downey, 2001; Goodman et al., 2012; Martin, 1995). Reviewing the evidence in both economics and evolutionary ecology, Lawson and Borgerhoff Mulder (2016) argued that fertility control in post-demographic-transition societies can be interpreted as an "offspring quality" strategy, which promotes descendant socioeconomic success by concentrating parental investment on fewer

children. Very few studies, however, directly demonstrate this dilution of parental investment. For instance, in one longitudinal study, Lawson and Mace (2009) found that parental investment (defined as maternal and paternal involvement in key activities) per child was negatively associated with sibship size regardless of family SES. This seems to indicate that even in affluent families, investment in offspring quantity might trade off with investment in offspring quality due to the dilution of parents' time and energy.

Not all aspects of offspring quality might be negatively affected by increasing offspring quantity. In humans and some other primates, social mechanisms and alloparenting might compensate for the fitness costs of the dilution of parental investment and increased sibling competition. Older siblings can contribute to childcare, subsistence, and teaching surviving skills, whereas co-residing adult siblings and kins can provide mutual aid and protection (Draper & Hames, 2000; Hill et al., 2011; see Del Giudice, 2020 and Lawson & Borgerhoff Mulder, 2016). Research also found that growing up with siblings generally promotes social competence and relationship qualities (Downey & Condrón, 2004; Merry et al., 2020). Overall, it appears that, in humans, the observed costs of prioritizing offspring quantity are mainly related to the dilution of socioeconomic resources (food and wealth) and parental care with increased fertility, which does not necessarily compromise all aspects of offspring quality due to the existence of social compensation mechanisms.

Mating Versus Parenting Effort

In sexual-reproducing species like humans, mating efforts (i.e., time and energy invested in searching for and securing copulations with mates) are essential for reproductive success. Mating activities may involve considerable energy and time expenditures (e.g., waiting for suitable mates, costly displays in courtship, competition with rivals, and mate guarding; Geary, 2000; Hill & Kaplan, 1999). A trade-off thus arises when mating efforts result in the diversion of time and energy away from parental investment (i.e., time and energy invested in enhancing the survivability and competitiveness of existing offspring that reduce the ability of parents to invest in additional offspring; Trivers, 1972). This trade-off is presumed to be particularly relevant to

males (or whichever sex experiencing stronger sexual selection; Kokko & Jennions, 2008). Theoretically, males have the incentive to escape from parental investment and maximize their fitness by finding more mates, unlike females who are constrained by higher reproductive costs and have less to gain from extra mating efforts (Trivers, 1972). On the other hand, paternal investment has been shown to facilitate the survival, health, and competitiveness of offspring in humans (Geary, 2000; Marlowe, 2000), which should boost the fitness payoff for males if paternity certainty is high.

More recently, theorists have begun to question the mating-versus-parenting trade-off as a given (Stiver & Alonzo, 2009). The complex dynamic of sexual selection and social interactions between sexes might weaken the trade-off even for males. For example, female preference for caring fathers (Lu et al., 2017) might lead to the male-male contest that drastically reduces the payoff of escaping parental duties. To achieve the optimal strategic balance between mating and parenting efforts, individuals might seek to strategize mate preferences, interactions with mates, and even their roles in shaping social institutions and norms regulating marriage and residence patterns (Lawson & Borgerhoff Mulder, 2016). Parents are less likely to escape from parental investment in circumstances where offspring survival and development are sensitive to parental care or when socially imposed conventions restrict extra-pair mating and childbirths. These circumstances would diminish the mating-versus-parenting trade-off and sex-role divergence (Kokko & Jennions, 2008). Conversely, in environments where mortality is “extrinsic” (i.e., “not sensitive to changes in reproductive decisions”; Stearns, 1992, p. 182), the payoff of parenting efforts is drastically reduced (Quinlan, 2007). In such circumstances, engaging in more short-term mating or finding mates with superior genetic quality might contribute more to fitness than long-term pair bonding and parental investment (Gangestad & Simpson, 2000). Thus, extrinsic risks are conducive to a stronger mating-versus-parenting trade-off. However, such a trade-off has differential payoffs for the two sexes, with men benefiting more than women do from prioritizing mating over parenting, and women benefiting more than men do from bonding with a high-quality mate as protector and provider. Such sex differences in the payoffs of mating and

parenting strategies might have contributed to cultural norms for traditional sex roles and greater tolerance of gender inequality, especially among males (Zhu & Chang, 2019). Indeed, evidence shows that people in countries with higher extrinsic risks tend to support traditional sex roles to a greater degree and show greater gender divergence in sexist attitudes. Countries with higher adult mortality rates are also less egalitarian in gender status, and these effects are mediated by total fertility (Zhu & Chang, 2020).

Summary of LH Trade-offs in Humans

The four basic LH trade-offs discussed above represent different conceptualizations of the mechanism of LH variations and sources of developmental plasticity (Del Giudice et al., 2015; Ellis et al., 2009). Partly based on Geary's (2002) partitioning of different fitness components, we propose a descriptive model of LH trade-offs in humans (Figure 1) that encompasses the aforementioned basic LH trade-offs. Total bioenergetic resources throughout the life course are first allocated to two overarching fitness components: somatic efforts and reproductive efforts. This trade-off is somewhat overlapping with the trade-off between current and future reproduction, with somatic efforts mainly contributing to future reproduction and reproductive efforts mainly contributing to current reproduction. However, "future reproduction" strategies also include delays of reproduction that do not necessarily involve somatic investment. Within somatic efforts, time and energy can be allocated to growth (including growth quality and growth speed investment) and/or maintenance. Within reproductive efforts, time and energy can be allocated to offspring quantity and/or offspring quality, both can be achieved by various mating and parenting efforts. Trade-offs can occur whenever different allocations draw from the same type of bioenergetic resource, with allocations downstream affected by allocations upstream (e.g., a lack of overall investment in somatic efforts should lead to more acute trade-offs between growth and maintenance).

The model illustrated in Figure 1 also considers features that might be of unique importance to humans. Human LH comprises many coevolved features such as long lifespan, prolonged juvenile development, extensive parental care and provisioning, and sophisticated

socio-cognitive processes (Del Giudice et al., 2015; Kaplan & Lancaster, 2003). For humans and other animals with prolonged development and learning, growth investment does not merely promote somatic growth speed in preparation for future reproduction but also improves growth quality that increases future energy “income” (e.g., development of skills that promote the efficiency of foraging or social negotiations for favorable resource distribution; Del Giudice et al., 2015).

It is also important to note that, for humans, not all bioenergetic resource expenditures are directly related to the fitness components illustrated in Figure 1. For example, adults (and older juveniles) spend a considerable amount of time and energy on material resource accumulation. Individuals might also allocate resources to help relatives or even unrelated others, as cooperativeness and altruism are an integral part of human sociality, driven by kin selection, reciprocity, and social selection (Fehr & Fischbacher, 2005; Nesse, 2007; Nowak & Sigmund, 2005). These energetic expenditures might indirectly affect life-history trade-offs and future reproductive success by generating additional bioenergetic resource income (e.g., better nutrition intake, higher social status).

Environmental Risks and Their Effects on LH Strategy in Humans

Researchers have long sought to explain the roles of physical and social aspects of ecological environments in shaping cross-society diversities and individual differences in developmental outcomes (Bronfenbrenner & Morris, 1998; Dall et al., 2004; Sng et al., 2018). From the perspective of LHT, human LH strategies and the underlying LH-related traits should be highly sensitive to environmental conditions (Ellis et al., 2009). This is because environmental variations over evolutionary time cause changing optimal points in LH trade-offs (a type of “variable selection”; see Del Giudice, 2020), such that no single phenotype or strategy would excel in all conditions. This, combined with the unique human LH with prolonged development and diverse habitats, renders developmental plasticity advantageous over invariant development (Del Giudice et al., 2015; Ellis & Del Giudice, 2019). The LH literature focuses on several key aspects of environmental risks that affect the payoff of different LH strategies and

shape developmental plasticity, including the level of morbidity–mortality threats, intraspecific competition, resource scarcity, and unpredictability (Del Giudice et al., 2015; Ellis et al., 2009).

Effects of Morbidity-Mortality Threats

Morbidity-mortality threats (e.g., predators, accidents, disasters, pathogens, and intraspecific violence) exert considerable selective pressure on human evolution. It is estimated that almost half of children in hunter-gatherer societies—resembling the human environment of evolutionary adaptedness—perish before reaching adulthood (Kaplan & Lancaster 2003; Volk & Atkinson 2013). In modern society, morbidity-mortality threats (often associated with low SES or dangerous living conditions) also impose considerable costs on physical and mental health as well as reproductive success (reviewed by Ellis et al., 2009). Ellis and colleagues (2009) posit that harshness (i.e., age-specific rates at which external factors cause morbidity-mortality in a population) should generally favor accelerated LH characterized by earlier maturity (in juveniles) and current reproduction (in adults) when individuals have enough embodied resources. However, the exact LH effects of harshness are theorized to be contingent on population density (competition) and whether it can be avoided or attenuated by personal or parental resource allocation (Baldini, 2015; Ellis et al., 2009). Specifically, when external morbidity-mortality threats are buffered by parental investment in juveniles, it would be beneficial to prioritize somatic investment over early reproduction. When juvenile-specific morbidity-mortality threats are insensitive to parental investment, however, rapid growth and early reproduction would be preferred (Ellis et al., 2009).

Largely consistent with the theoretical predictions, a longitudinal study using 125 women in a rural Caribbean community showed that both infant mortality rate (IMR) and population mortality rates at age of maturity exhibited a quadratic association with earlier reproduction (Quinlan, 2010). The data also showed that extrinsic mortality after the age of maturity only had significant effects on reproductive timing when IMR was moderate or low (Quinlan, 2010). It is also possible that individuals' LH strategy is not affected by mortality rates per se but is responsive to environmental cues (adverse personal experiences or experiences of important

others) that are related to morbidity-mortality in the ancestral environments (Del Giudice, 2020; Ellis et al., 2009). However, in reality, these cues are often inseparable from other aspects of environmental risks, such as competition, resource scarcity, and unpredictability.

Effects of Competition

In environments with high levels of within-population competition, individuals' fitness depends not only on their own resource allocation but also on that of others (Zhu et al., 2019). In evolutionary biology, researchers distinguished between the concept of *contest competition* (i.e., individuals have differential access to the resources critical for survival and reproduction) and *scramble competition* (i.e., individuals equally partition resources; Hassell, 1975; Nicholson, 1954). The former is more appropriate than the latter to describe human competition (Ellis et al., 2009).

It is important to distinguish between the effects of contest competition and the effects of over-crowding, both associated with high population density (Sng & Ackerman, 2020). Over-crowding has been linked to pathological outcomes in humans and animals (Calhoun, 1962; Galle et al., 1972), though the adverse effects on humans typically disappear when factors related to resource scarcity are taken into account (Sng & Ackerman, 2020). Conversely, contest competition should be conducive to late reproduction and offspring-quality investment (MacArthur & Wilson, 1967; Sng & Ackerman, 2020; Sng et al., 2017). An intuitive explanation is that densely populated environments entail intense competition, and for offspring to outperform others, parents have to increase their investment in offspring quality at the expense of offspring quantity (Ellis et al., 2009; Mace, 2000; Sng & Ackerman, 2020). Therefore, in humans, high population density should favor future-oriented investment in growth quality and offspring quality that boost individuals' competitiveness, which is conducive to slow LH strategies. Supporting this view, Sng et al. (2017) examined both population-level and individual-level effects of density on variables reflecting LH strategies. They found that, across countries and the 50 U.S. states, densely populated countries and states have lower fertility, older marrying age, more commitment to long-term relationships (rather than casual short-term

relationships), and increased investment in education (Sng et al., 2017). Further, participants exposed to information about increasing crowdedness showed stronger future orientation and preferences for fewer children and romantic partners (linked to offspring quality and reduced mating efforts; Sng et al., 2017).

The behavioral and psychological effects of competition are highly diverse. Contest competition may take hostile forms such as aggressive assertions of dominance or territoriality (Ellis et al., 2009), which leads to reduced carrying capacity or lower average fitness due to costly fighting and/or reduced energy efficiency of larger body sizes (Mueller, 1997; Wright et al., 2019). Indeed, higher population densities are associated with higher mortality rates in forager societies (Walker & Hamilton 2008). However, contest competition may also facilitate competitive altruism, which might boost carrying capacity or enhance overall fitness in some circumstances (Nesse, 2007; Nowak & Sigmund, 2005). Zhu et al. (2018) showed that participants' experiences and evaluation of educational and occupational competition positively predicted investment in empathic concern, intimate relationships, perspective-taking tendencies, and planning skills. These traits, in turn, predicted other-oriented moral reasoning and judgments (Zhu et al., 2018).

Another important aspect of competition has to do with its effects on strategic plurality. Contest competition tends to generate individual differences in access to bioenergetic resources (including mating opportunities) and fitness (Ellis et al., 2009). The level of competition typical in modern society is likely to favor the diversification of LH strategies based on individuals' resource endowment (e.g., reflected in childhood SES). Individuals facing severe competitive disadvantages (e.g., poor people living in slum districts) might benefit from a quantity-focused strategy that promotes immediate reproductive output without investing too much in marginal gains of competitiveness. Individuals with uncontested competitive advantages (e.g., offspring of billionaires or celebrities in modern society), by contrast, can afford to invest in a quality-and-quantity LH strategy. Most individuals in between would still benefit from a quality-focused LH strategy.

There is some empirical evidence compatible with this strategic plurality argument. For instance, individuals with wealthier childhoods, compared with those with poorer childhoods, felt more sense of personal control in response to economic uncertainty cues (potentially linked to more intense resource competition). Personal control also mediated the relationship between economic uncertainty cues and traits such as impulsivity and low task persistence (indicating low investment in the future) among participants with lower (but not higher) family resources in childhood (Mittal & Griskevicius, 2014). One recent study showed that exposure to competitive cues (about educational and occupation contests) increased participants' monetary donation in a spontaneous donation task among high-income participants but decreased the amount of donation among low-income participants (Zhu et al., 2019, Study 1). This finding indicates that individuals' resource allocation responses are indeed contingent on both resource endowment and cues of competition. However, there is currently a lack of research on the diversifying effects of moderate levels of competition in developmental psychology.

Effects of Resource Scarcity

In humans, external resource scarcity might be mediated by both external environments (e.g., family income and parental provisioning) and internal states (e.g., health and nutritional status; Chang & Lu, 2018; Chang et al., 2019a). In empirical research, resource scarcity is often conflated with morbidity-mortality threats, as they are often positively correlated with each other and both associated with socioeconomic adversity (competitive disadvantage) in industrialized societies (Ellis & Del Giudice, 2019). However, different degrees of resource scarcity might cause morbidity-mortality in different ways and lead to opposite predictions.

Specifically, *absolute resource scarcity* that severely constrains one's nutritional intake might cause amenorrhea, which reduces fertility and depress the immune functions, which impairs individuals' survivability. Consequently, absolute resource scarcity that is not buffered by parental care or social support might indirectly cause morbidity-mortality (e.g., due to irreversible impairment through prolonged malnutrition and starvation) that can only be mitigated by economizing energy expenditures. Absolute resource scarcity should lead to an

“energy-sparing phenotype” that reduces all types of fitness investment to various degrees, leading to slower growth, poorer health, delayed sexual maturation, and reduced reproductive regardless of the level of morbidity-mortality (Ellis et al., 2009). By contrast, low SES likely reflects *relative resource scarcity* (competitive disadvantages), which is sometimes accompanied by morbidity-mortality threats (when poverty is correlated with neighborhood insecurity). As extrapolated earlier, relative resource scarcity should favor a quantity-focused, fast-and-cheap strategy. Consistent with the pattern of absolute resource scarcity, a meta-analysis on the timing of puberty showed that delayed menarche is associated with lower adult stature in resource-scarce traditional societies. However, the opposite pattern was found in industrialized societies, which likely conform to the pattern of relative resource scarcity (McIntyre & Kacerosky, 2011).

In support of the distinction between absolute resource scarcity and other sources of morbidity-mortality, Quinlan’s (2010) rural Caribbean data showed that extremely high infant mortality rates (IMR), probably caused by absolute resource stress that leads to maternal somatic depletion, were found to be associated with delayed, rather than earlier age at first reproduction. Moderate levels of IMR, by contrast, led to earlier maturity and first reproduction than low IMR (Quinlan, 2010). In industrialized societies, lower childhood SES or racial groups associated with low SES (both indicating relative resource scarcity) are also typically associated with fast LH strategies (e.g., Holdsworth & Appleton, 2020; Mishra et al., 2009; Sheppard et al., 2016). Griskevicius and colleagues (2011a, 2011b, 2013) showed that low childhood SES is associated with behavioral traits supporting a fast-and-cheap phenotype (e.g., increased temporal discounting of rewards, low task persistence, and preferences for earlier reproductive timing) in the face of experimentally manipulated cues of uncertain risks.

Effects of Unpredictability

According to the LHT framework, LH strategies also respond to the degree of environmental unpredictability or stochasticity (Ellis et al., 2009; Hastings & Caswell, 1979; Young et al., 2020). Like harshness (the mean level of morbidity-mortality threats), the effect of

unpredictability (variability in morbidity-mortality threats) is also age-specific (Ellis et al., 2009). When there is no absolute resource constraint, adult-specific unpredictability is expected to favor fast LH traits, e.g., prioritization of reproductive efforts, increased fertility, and shorter lifespan, (Hastings & Caswell, 1979; Ellis et al., 2009). By contrast, juvenile-specific unpredictability is linked to bet-hedging (Ellis et al., 2009; Starrfelt & Kokko, 2012), which is defined as reproductive strategies that lower the genotypic variance of offspring fitness across possible environmental conditions, essentially reducing the potential negative impacts of environmental variability (Starrfelt & Kokko, 2012). This can be achieved in two ways:

A conservative bet-hedging strategy produces “generalists” offspring that have a moderate level of adaptation to all possible environments (e.g., dry or wet environments), thus preventing the worst-case scenario where all descendants are ill-adapted to the environment (e.g., drought-resistant phenotypes born into a wet environment; Byrne & Keogh, 2009). *A diversified bet-hedging strategy*, by contrast, produces diversified clutches of “specialists” for various possible environments so that at least some of them are highly adaptive to the future environment (despite the others being poorly adapted; Starrfelt & Kokko, 2012).

Depending on the time scale of environmental variability, bet-hedging can be based on either genetically determined development in response to between-generation variability (i.e., descendants of the same generation only experience one type of environment, often equated with temporal variability) or plastic responses (e.g., differential parental investment, offspring dispersal) to the within-generation variability (often equated with spatial variability; Starrfelt & Kokko, 2012). Differential parental investment in offspring (including material wealth inheritance) is quite common in human society. When parents are uncertain of how many children (of what quality) can survive to adulthood and have their own children (to be worthy of inheritance of parental wealth), they tend to unevenly distribute parental investment favoring older children or heirs who are entitled to inherit wealth (Lawson & Borgerhoff Mulder, 2016). This “heirs and spares” strategy is commonly practiced by parents in many developing societies

in the form of son-preferring gender differences in parental investment (Das Gupta et al., 2003; Pande, 2003; see Lawson & Borgerhoff Mulder, 2016).

Empirical Support for the Effects of Environmental Risks

The work on the environment-contingent developmental plasticity of LH strategies has been fruitful over the past few decades. Several key models provided a relatively solid theoretical ground for hypothesis-testing regarding the effects of morbidity-mortality threats, competition, resource-scarcity, and unpredictability on human LH strategies (e.g., Ellis et al., 2009) or broader ecological effects on behavioral, psychological, and cultural outcomes (Sng et al., 2018). A growing number of studies have documented the effects of early, chronic exposure to environmental risks on the development of behavioral, cognitive, and social traits.

Longitudinal studies and studies using retrospective self-reports showed that early experiences of harshness and unpredictability are linked to increased sexuality in adolescence (Belsky et al., 2012; Brumbach et al., 2009), deviant and risky behaviors in adolescence and young adulthood (Brumbach et al., 2009; Simpson et al., 2012), increased aggression and impulsivity (Chang et al., 2019a, 2019b), academic underperformance (Chang & Lu, 2018), externalizing problems and substance uses (Doom et al., 2016), cognitive tolerance of deviance and willingness to engage in risky sex (Gibbons et al., 2012), self-centered moral judgments (Zhu et al., 2018), preference for dominance-based leadership (Zhu et al., 2022), and intuitive (as opposed to deliberate) cognitive styles (X. R. Wang et al., 2022).

However, the LH research on environmental effects also generates a lot of mixed and unexpected findings that prompt researchers to revise or re-interpret existing models. Some of these issues may stem from ambiguities in the conceptualization of environmental risks and operationalization in empirical measurement (Copping et al., 2014; Sear, 2020; Stearns & Rodrigues, 2020). In evolutionary psychological studies, harshness has been operationalized as self-reported exposure to violence from conspecifics (Brumbach et al., 2009), low income-to-needs ratio (Belsky et al., 2012), or low SES (Simpson et al., 2012; Szepeswol et al., 2019). Unpredictability has been operationalized as changes or inconsistencies in life (e.g., household

moves, paternal transitions, taken by social services; Belsky et al., 2012; Brumbach et al., 2009; Szepeswol et al., 2017, 2019), accumulated frequency of uncontrollable, stressful life events (Chang et al., 2019a, 2019b; Zhu et al., 2018), or family income changes (Chang et al., 2019a, 2019b). In other cases, measures of morbidity-mortality threats do not explicitly distinguish between harshness and unpredictability, such as neighborhood insecurity and family chaos (Chang et al., 2019a, 2019b), pathogen pressures (Lu et al., 2021), or worries about intergroup violence (Zhu & Chang, 2020; Zhu et al., 2021).

Empirical measures of harshness and unpredictability inevitably overlap with resource scarcity (especially when they are represented by low SES). The fact that different degrees of resource scarcity are linked to distinct LH strategies (Ellis et al., 2009) highlights the need to distinguish between absolute and relative resource scarcity. Density-dependent contest competition might also be implicitly involved in some measures of morbidity-mortality threats (e.g., violent conflicts and pathogen stress). Although density-dependent factors are often incorporated into theoretical and mathematical models (e.g., Baldini, 2015; Ellis et al., 2009; Wright et al., 2019), very few empirical studies in evolutionary psychology measured competition as a separate dimension of environmental risks (e.g., Sng et al., 2017; Zhu et al., 2018). In these studies, competition is represented by demographic data of population density (Sng et al., 2017) or perceived educational and occupational competitive pressures (Zhu et al., 2018). Future empirical research should continue the exploration of the effects of density and competition while also taking into account the possibility of strategic plurality due to interactions between competition and resource endowment.

Developmental Calibration of LH Strategy

LH strategies are not simply products of external ecological stress. The developmental calibration of LH strategy is sensitive to both environmental and genetic factors, which lead to developmental outcomes through multiple intermediary processes. These developmental processes include early attachment security in response to familial context and caregiving experiences (Belsky et al., 1991; Chisholm, 1996; Del Giudice et al., 2015), the configuration of

stress response systems (including autonomic, adrenocortical, and immune signaling; Del Giudice et al., 2011; Ellis & Del Giudice 2019), internal schemas and worldviews (de Baca & Ellis, 2017), and development of executive functions (e.g., self-inhibition of impulsivity, planning for long-term gains; Figueredo & Jacobs, 2010; Figueredo et al., 2006, 2012). The individual differences produced by these plastic developmental processes constitute LH-related traits, which ultimately contribute to fitness indicators and LH strategies at the population and species levels (Del Giudice, 2020).

The LH perspective has inspired developmental psychologists to rethink the role of early adversity in familial contexts, which is of special concern due to the extensive biparental care in humans (Geary, 2000). Specifically, the psychosocial acceleration theory (PAT; Belsky et al., 1991; Belsky, 2012, 2019) maintains that early stress represented by insensitive rearing may be seen as proxies of adverse external ecological conditions. Children's early attachment security, functioning as an internal working model for the calibration of human LH strategies (Belsky et al., 1991), is sensitive to the experiences of parental care and family dynamics. This environmentally sensitive developmental process serves to match individuals to their environment in a manner that promotes fitness across various ecological conditions. Specifically, familial proxies of harshness and unpredictability are linked to the development of a schema of a dangerous and unpredictable world (de Baca & Ellis, 2017), as well as accelerated LH traits such as earlier pubertal timing, earlier sexual debut, unstable pair bonding, and low investment in social resources (Belsky, 2012; Belsky et al., 1991). A similar model proposed by Chisholm (1993, 1996) also maintains that different attachment styles may be seen as children's developmental responses to risk and uncertainty, which are functions of trade-offs between parents' reproductive and parenting efforts.

Consistent with the predictions of these models, past research has shown that both childhood adversities (e.g., resource insecurity, child abuse, lack of family warmth, familial conflicts, father absence, childhood exposure to violence or natural disaster) and early insecure attachment predicted earlier pubertal maturation (Belsky et al., 2010; Ellis, 2004; Lian et

al., 2018; Magnus et al., 2018; Webster et al., 2014; reviewed by Ellis & Del Giudice, 2019). A recent meta-analysis showed that childhood stress robustly mediated the relationship between father absence and early menarcheal timing (Guo et al., 2020). However, research also showed that the acceleration effects of environmental harshness and unpredictability experienced in the first 5 years of life on puberty timing may be partly buffered by parental care and secure attachment (Sung et al., 2016). There is also evidence that parenting quality mediated the relationship between various types of early adversity and behavioral outcomes (e.g., increased sexuality, insecure romantic attachment, low parental investment in men, involvement in intimate partner violence) by adolescence and adulthood (Belsky et al., 2012; Szepeswol et al., 2015, 2017, 2019). Some of the “accelerated” behavioral traits might be mediated by unpredictability-driven worldviews derived from early experiences of low parental investment (de Baca & Ellis, 2017). For example, children with mothers who devote more to mating and less to parenting scored higher on the unpredictability schema (de Baca et al., 2016).

According to PAT, accelerated LH strategies would also incur costs on individuals’ mental and physical health, partly through health-related behaviors and symptoms that are deemed “maladaptive” by classic models of psychosocial dysregulation (e.g., Shonkoff et al., 2012; reviewed by Ellis & Del Giudice, 2019). However, from the LH perspective, these behaviors and dysregulations might be considered “adaptive” in the sense that they contribute to the reproductive strategies that, on average, enhance fitness in adverse circumstances (Del Giudice et al., 2011; Ellis & Del Giudice, 2014, 2019). The PAT and other LH-calibration models are thus able to account for links between reproductive strategies and health outcomes. For example, using a representative adult sample from France, Mell et al. (2018) reported that harsh childhood environments predicted earlier age at first childbirth and earlier age of sexual debut. Earlier age at first childbirth, in turn, was related to poorer health, whereas earlier sexual debut was associated with smoking habit and reduced health-maintaining efforts (Mell et al., 2018). The LH reasoning has also been extended to explain patterns of psychopathology (Del Giudice, 2014, 2015). Del Giudice and colleagues argue that psychopathological symptoms

might stem from both maladaptive dysfunctions and adaptive mechanisms in response to undesirable conditions (their adaptiveness should be evaluated at both the population and individual levels; Del Giudice, 2018; Del Giudice & Haltigan, 2021).

The PAT framework has since been updated, integrating the calibration of neurophysiological pathways and immune systems that give rise to certain reproductive strategies and (physical and mental) health statuses (de Baca & Ellis, 2017; Ellis & Del Giudice, 2019). Seeking to account for more fine-grained patterns of LH calibration in response to ecological stress, the adaptive calibration model (ACM) proposed by Del Giudice and colleagues (Del Giudice et al., 2011; Ellis & Del Giudice, 2019) focused on the stress response system (SRS) as a key mediator of human LH variations. The SRS consists of the autonomic (sympathetic and parasympathetic) nervous system (ANS) and the hypothalamic-pituitary-adrenal (HPA) axis. It not only regulates short-term physiological and behavioral responses to threats in the current environment but also codes environmental information for longer-term adaptive calibration of LH traits, especially at different transition points between developmental stages. Del Giudice et al. (2011) identified four different SRS profiles with varying ANS and HPA activation patterns (i.e., responsiveness and recovery speed) and associated behavioral characteristics—sensitive, buffered, vigilant, and unemotional—that are adapted to low, moderate, high, and extremely high environmental stress levels, respectively. The ACM also predicts sex differences in the reactions to high adversity (Ellis & Del Giudice, 2019). Consistent with such prediction, past research showed that maltreated boys are more likely to show blunted cortisol reactivity than maltreated girls, whereas girls with childhood adversity are more likely to show heightened cortisol reactivity than boys (e.g., Fearon et al., 2017; Trickett et al., 2014). Overall, the aforementioned LH calibration models have provided novel explanations for empirical evidence regarding stress responses, health outcomes, and their links to reproductive strategies (reviewed by Del Giudice et al., 2011 and Ellis & Del Giudice, 2019). However, predictions derived from these models are yet to be systematically tested with longitudinal

studies that incorporate measures of neuroendocrine and immune functioning and control for genetic effects (Del Giudice, 2020).

Outstanding Questions and Future Directions

Recent decades have seen the departure of LH research in evolutionary psychology from LH research in evolutionary biology (Nettle & Frankenhuis, 2020; Sear, 2020). The former field, although sharing core tenets about basic LH trade-offs and environmental effects with the latter, focused on aspects of environments, development, and outcomes that are of unique importance for humans. However, some assumptions that are taken for granted in LH research in evolutionary psychology are not so certain from the perspective of evolutionary biology.

To begin, LH research in developmental psychology typically assumes variations in LH-related traits without explicitly formulating their potential genetic underpinning. In particular, it is largely in debate whether balancing selection (i.e., systematic changes in the direction of selective pressures across individuals, space, or time) can and does maintain genetic variation in LH traits (see Del Giudice, 2020 and Zietsch & Sidari, 2020 for detailed discussion). Another key assumption of psychological models of human LH strategy is adaptive developmental plasticity (Del Giudice et al., 2015), which implies a relatively low contribution of genetic factors compared with environmental factors. This, however, seems to be at odds with behavioral genetics findings indicating a high heritability of LH-related traits (Zietsch & Sidari, 2020). Unfortunately, most human developmental studies lack control for potential genetic confounding in the association between early environmental conditions with later outcomes (see Barbaro et al. 2017). More studies with designs to separate genetic factors from environmental factors are needed to address this question about the degree of adaptive developmental plasticity.

A third issue for the LH research in developmental psychology lies in the implicitly or uncritically endorsed assumption of parallel mechanisms operating at different levels of analysis. This leads to the expectation of similar patterns of LH variations both between and within species when similar LH trade-offs are at play (Del Giudice, 2020; Jeschke et al., 2008; Réale et al., 2010). However, such cross-level similarity should not be taken for granted (for in-depth

discussion, see Baldini, 2015; Del Giudice, 2020; Zietsch & Sidari, 2020) and it conflates evolutionary processes that select for species-level LH variations and developmental processes that give rise to individual-level plasticity (Del Giudice, 2020; Zietsch & Sidari, 2020). Association between a certain trait and certain environmental risks (or between traits) at the population level might not be observed at the individual level, due to random stochastic factors, measurement errors, individual differences in the susceptibility to external stimuli, and complex interplays among traits (summarized by Del Giudice, 2020). It is therefore important for LH research in psychology to explicitly formulate their hypotheses at the same level as the theoretical LH mechanism invoked to support the hypotheses.

The final question has to do with the role of the fast-slow paradigm in LH research. The ambiguous conceptualization of the fast-slow continuum tends to generate implausible or unjustified expectations of positive correlations among “fast” or “slow” traits, especially in LH research that adopts the “psychometric” approach (Sear, 2020). This approach essentially extrapolates the “evolutionary functions” of behavioral traits from the pattern of trait-trait correlations, largely overlooking the possibility of age-specific development and complex functional relations among different LH-related traits (Del Giudice, 2020). For instance, investing in growth speed in childhood at the cost of future health might be seen as a “fast” strategy, whereas continued investment in growth in adulthood at the cost of current reproduction might be seen as a “slow” strategy. It is also possible that two LH-related traits (e.g., extensive mate search and extensive parental care) that independently contribute to the same LH strategy (e.g., offspring quality) might trade off with each other in the same context. As a way forward, Sear (2020), among others, suggests placing more emphasis on understanding LH trade-offs rather than a psychometric conceptualization of LH strategies. In many cases, individuals appear to mix characteristics of fast and slow strategies at different life stages in adaptive ways. Consequently, human LH is perhaps best described as constituting multiple developmental stages (Del Giudice & Belsky, 2011) and varies along multiple continuums representing fitness investment at various stages, which are constrained by different basic trade-offs. Research should

explicitly formulate the costs, benefits, and constraints of LH-related traits (and the fitness investment it represents) in contexts (for a similar argument, see Del Giudice, 2020). This is especially important for inquiries of behavioral traits, whose expression is often contingent on interactions among chronic experiences, resource availability, and situational cues (e.g., Griskevicius et al., 2011a, 2011b; Zhu et al., 2019).

Conclusion

The present review seeks to unravel the intricate links between the evolutionary biological background of LHT and LH research in evolutionary psychology. LH research in evolutionary psychology is still at an early stage, lacking a well-established theoretical framework and comprehensive instruments for assessing environmental risks as well as traits related to different LH strategies at the individual level (see Del Giudice, 2020). Still, the models of LH trade-offs, environmental effects, and developmental calibration processes (e.g., PAT and ACM) reviewed above provided a strong starting point for future research on individual differences and developmental processes from the LH perspective.

One reason for the integration between LHT and the research on human development is that the former allows a unifying understanding of wide-ranging human behaviors and their interconnections not as segregated developmental outcomes but within the contexts of evolutionary, familial, developmental, and micro-developmental processes. The LH approach also addresses a common misunderstanding, namely what is evolved must be fixed in our genes. Contrary to this view, the LH perspective allows us to test hypotheses about developmental plasticity and conditional expression of behavioral traits at many different levels. One such example is the LH account of individual differences and cross-society variations in sex role distinction and gender equality across different environments (Kokko & Jennions, 2008; Zhu & Chang, 2019, 2020).

The complexity of LH variations and their mechanisms in humans place extra requirements on the theoretical and operational clarity for LH research in evolutionary psychology. Specifically, it is vital to pinpoint the specific LH trade-offs, intermediary processes,

and potential confounding factors that, together, influence the ultimate outcomes in question. Human LH research would also benefit considerably from multidisciplinary approaches ranging from the measurement of various physiological signaling as a part of the SRS response to the use of genomic sequencing to identify relevant genes (e.g., X. T. Wang et al., 2013; for review see Bolund, 2020). In all, building on interdisciplinary knowledge of evolutionary biology, neurophysiology, and developmental sciences, LH research in evolutionary psychology not only provides new insights into some familiar phenomena but also generates novel, testable hypotheses that might slowly change how we view the world.

Conflict of Interest: The authors declare no conflict of interest.

Acknowledgements: We thank Dr. Marco Del Giudice and an anonymous reviewer for critically reading the manuscript and suggesting substantial improvements.

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Figure Caption:

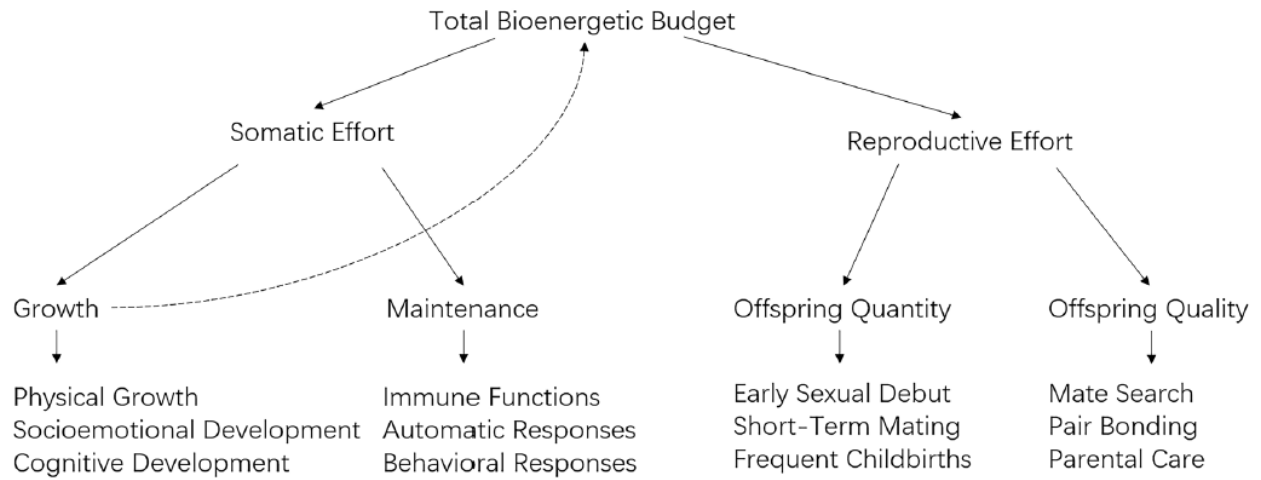


Figure 1 A descriptive model of multiple levels of LH trade-offs. Solid straight-line arrows represent the allocation of bioenergetic resources (time and energy), and dashed curved arrows represent the feedback contributions of growth (including development and learning) to the total bioenergetic budget.