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# What is essential for life and life history research?

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#### **Abstract**

The featured article introduces a much-needed theoretical framework for developing a dual-process model of life history calibration. This model accounts for the counterbalancing effects of individual energetic stresses and extrinsic mortality threats of the environment. This framework also reinstates resource availability – a key determinant of energetic conditions – into life history research, resolving its previous exclusion due to similar countervailing influences relative to extrinsic mortality threats.

What is essential for life? The answer is food or resources and safety or freedom from extrinsic mortality (EM). However, human life history (LH) research has historically focused almost exclusively on EM, largely neglecting the roles of resource and population density. That is set to change with the publication of the featured article, in which Ellis, Reid, and Kramer (2024) introduce a two-tiered LH model proposing that environmental influences on human LH strategies operate through two distinct pathways: an energetic pathway (Tier 1) and a second tier that transmits ambient

EM cues. The first tier immerses energetic stressors, such as marginal nutrition, which constrain growth, pubertal development, and adult reproductive function. In contrast to the typical effect of ambient EM cues that accelerate LH, these energetic stressors induce trade-offs that divert energy away from growth and reproduction. The result is delayed sexual maturation, a measured reproductive pace, and fewer offspring - traits characteristic of slower LH. Although these conditions are framed as internal and biological, they stem and derive from resource availability in the external environment. Thus, the significance of the featured article lies in its reintroduction of a long-neglected, yet critical, density-dependent variable - resource - into human LH research. Separately, how does this two-tiered model differ functionally, though not necessarily conceptually, from the internal predicted adaptive response model, or internal PAR (Nettle & Bateson, 2015; Nettle, Frankenhuis, & Rickard, 2013), which incorporates both external environments and the body's enduring physiological conditions as cues for LH calibration?

#### Repatriating resource into life history research

Originally conceptualized within r/K selection theory – before EM took center stage - LH was conceived to be primarily influenced by population density and the resulting intraspecific competition for resources necessary to support population growth (MacArthur & Wilson, 1967; Pianka, 1970). Low-density, resource-rich "r" environments were thought to favor faster LH traits, characterized by accelerated growth and maturation, early and frequent reproduction, and large numbers of offspring receiving minimal parental investment, as energy was diverted toward mating efforts. In contrast, high-density, resource-limited "K" environments were believed to favor slower LH strategies, including delayed growth and reproduction, fewer offspring, and greater parental investment. These density-dependent processes, conceptualized at the species or population level, correspond to the individual-level energetic outcomes described in the two-tiered model by Ellis et al. (2024). The link between resource availability, population density, and EM mirrors the relationship between energetics and EM in the twotiered model. Energetic stress has been evolutionarily tied to ambient EM cues as a primary historical driver of premature death (Ellis et al., 2024). While energetics establish the developmental baseline for growth and puberty, ambient cues exert secondary influences when energetic resources are sufficient. After puberty, the two tiers exert opposing forces on adult reproductive outcomes: energetic constraints may suppress fertility, while EM cues may enhance it. Similarly, in r/K theory, high population density reduces per capita resource availability and thereby energy intake, while increasing EM through workings of intraspecific violence, infectious disease transmission, and resource depletion itself. These dual pressures result in countervailing LH responses. Until Ellis et al. (2024), there had been no satisfactory explanation for such counterbalancing effects. As a consequence, LH research largely dismissed resource availability as a factor, arguing that it had diminished relevance in modern populations (Chang & Lu, 2018) or that EM was simply the more critical variable for LH calibration (Ellis et al., 2009). The twotiered model offers a robust theoretical framework that reinstates energetic condition - or resource availability - as a primary driver of human LH strategies.

### Comparing to other dual process models

Nettle and colleagues proposed the internal PAR model (Nettle & Bateson, 2015; Nettle et al., 2013), which differs from its counterpart, the external PAR model (Gluckman et al., 2005). Internal PAR posits that early environmental conditions such as food scarcity, disease exposure, and other stressors leave enduring biological imprints on an individual's somatic state - affecting body size, muscular strength, organ function, and general health. Like the two-tiered model, internal PAR views these lasting physiological changes as cues guiding adaptive developmental plasticity, ultimately shaping an individual's LH strategy. However, unlike the two-tiered model, internal PAR predicts that both compromised internal states and adverse external environments produce similar physical and behavioral phenotypes. Empirical tests of the model show that poor internal states (e.g., prenatal substance exposure, chronic illness) and harsh external environments (e.g., parental transitions, dangerous neighborhoods) during childhood both predict fast LH behavioral profiles, including risky sexual conduct, adolescent delinquency, and risk taking and impulsivity (Chang et al., 2019; Ellis et al., 2021; Hartman et al., 2017). Most notably, internal PAR predicts that somatic compromise accelerates pubertal development (Rickard, Frankenhuis, & Nettle, 2014), whereas the two-tiered model suggests it delays it (Ellis et al., 2024).

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# Operational and conceptual confusion in life history research necessitates the two-tiered model

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## **Abstract**

Our systematic analysis of operationalizations and conceptualizations of harshness (extrinsic mortality) and unpredictability in the (psychology) life history literature highlights that (1) employment of extremely diverse measures contributes to the confusion about the effect of harshness on life history traits and (2) few measures reflect energetic stress or ambient EM, such that Ellis et al.'s two-tiered model should motivate future research.

Ellis, Reid, and Kramer (this issue) present an elegant and powerfully explanatory two-tiered model for the seemingly disparate effects of extrinsic mortality (EM) on reproductive patterns constituting life history strategies. By distinguishing between sources of EM that reflect a lack of survival/energetic resources versus those that reflect the presence of cues of threat, the authors make sense of findings that EM can predict both faster life history strategies – i.e., sooner and more reproduction – and slower life history strategies – i.e., delayed sexual maturation. That is,