



Current debates in human life history research

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1. Current debates in human life history research

Animals are born, mature, reproduce, age, and die. These are the milestones; the rest are details. Some species complete this cycle in days, others over centuries. Some mature fast, others slow. Some have thousands of offspring (e.g., carp), others few (e.g., whales) (Stearns, 1992; Thorson, 1950). In fact, some animals barely seem to age and die mainly from extrinsic factors (e.g., naked mole rats) (Kupferschmidt, 2018; Ruby, Smith, & Buffenstein, 2018). Some die while giving birth, serving as their offspring's first meal; others die alone, not having seen their offspring in months or years. Nature is astonishing and macabre. To make things wilder, there is variation among individuals within the same population. Some mature faster than others. Some invest more in their offspring than others. Some reach old age, others die young. This variation may result from differences in genes, experiences, or both. This is life history and there are many puzzles to solve.

The integration of psychology with life history has deep roots, but in the past 15 years, the number of studies bridging these fields has increased rapidly (Nettle & Frankenhuis, 2019). This development has led to new ideas and methods. Early work focused on life history traits that directly affect fitness, such as the age at first reproduction, the number and size of offspring, reproductive lifespan, and ageing. Recent studies incorporate the idea that life history strategies also include physiological traits (e.g., metabolic rate) and cognitive traits (e.g., aggression, risk taking, and impulsivity). The early work focused mainly on variation between groups (species or populations). Recent studies often examine variation among group members, and in particular the hypothesis that there is a fast-slow continuum of individual differences, where faster individuals mature at a younger age, have more offspring, invest less in each offspring, and senesce and die earlier. The issues of how best to connect life history strategies to behavioral and physiological traits and how to apply it to individual, rather than population or species, differences are central to this special issue.

2. An overview of debates

The current issue addresses two specific sets of questions in these debates. The first set of questions concerns theory:

- Does theory predict a fast-slow continuum between groups of organisms (species or populations)? Does theory predict a fast-slow continuum between individuals from the same population? Are these predictions limited to life history traits, or do they include cognitive and physiological traits as well? How do answers to these questions depend on our assumptions, definitions, and notions of theory?

The second set of questions concerns the data:

- Do the data support a fast-slow continuum between groups of organisms (species or populations)? Do the data support a fast-slow continuum between individuals from the same population? Do the data support covariation among life history traits only, or among cognitive and physiological traits as well? How do answers to these questions depend on what we measure and how, and which species and populations we sample from?

The contributions to this issue provide very different answers to these questions. Our goal as Editors is not to tell readers what to think, but rather to offer a buffet of useful information that advances the field. This buffet is of course not a random collection, but a selection of viewpoints that we think should be part of the conversation. Hence the issue brings together anthropologists, psychologists, and biologists at different career stages and from different continents. At the same time, the issue is more limited in the perspectives it covers than it should be. We also need other views at the table.

To this end, we welcome submissions of commentaries on articles published in this special issue. To be considered, please submit a commentary proposal of no more than 500 words in which you detail the aspect of the paper(s) you intend to comment on. Please DO NOT submit a full commentary without an invitation to do so. Proposals will be reviewed by the Editors of the Special Issue and the Editor-in-Chief and will be selected based on the extent to which they advance the debates in the special issue, whether they provide a perspective that is missing from the special issue, and how well the arguments and evidence are presented. We anticipate publishing between 6 and 8 commentaries, but will decrease or increase this number based on the

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quality of submissions. In addition to this call for commentaries, we may invite commentary proposals from scholars based on their expertise and the desire to include a diversity of viewpoints (such invitations do not guarantee an invitation to develop the proposal into a full commentary). If you wish to contribute a commentary, please submit your proposal—and only your proposal—to Deb Lieberman (debra@miami.edu) by January 1st, 2021. Decisions will be made by January 15th and completed commentaries will be due by February 15th. Instructions for commentaries will be provided upon proposal acceptance. All completed commentaries will be reviewed and accepted or rejected based on quality by the Editors with the aim of publishing the collection in the 3rd issue of 2021.

3. The birth of the issue

This is one of the first special issues *Evolution and Human Behavior* in over two decades. The issue presents a coherent set of 10 articles, including this introduction. Our goal was to do more than develop a collection of papers on a theme. We wanted the articles to fit into a larger whole that is more than the sum of its parts. We had clear ideas about what topics each article should cover. Of course, authors were free to cover this topic as they saw fit. We expected that contributors would offer different perspectives, and they did. Through diversity comes insight: one perspective may show an elephant's tail, another its trunk; through both lenses, we see an elephant marching, gracefully, towards knowledge.

4. Does theory predict a fast-slow continuum?

The answer depends on who you ask. Some contributors argue that theory predicts a fast-slow continuum between groups and, to the extent that individual differences are the result of plasticity – the ability to adaptively tailor development to environmental conditions based on experience (Barrett, 2015; Stearns, 1989) – also among the members of a population (André & Rousset, 2020). Others claim that the field lacks theory to predict either continuum (Zietsch & Sidari, 2019). Still others contend that theory predicts a fast-slow continuum between groups under some conditions, but that there is no theory that predicts a fast-slow continuum among individuals (Stearns & Rodrigues, 2020). This disagreement raises a key question: in which conditions should we expect the same patterns of life history variation between and within populations or species?

A common theme across many of the papers is the need for more clarity on this question. André and Rousset (2020) present a formal model showing that facultative developmental responses often match the responses of population mean values. By contrast, Stearns and Rodrigues (2020) present a formal model showing that the predictions can be in opposite directions. Del Giudice (2020) argues that although current theory is limited, there are good reasons to employ the ‘ecological gambit’, i.e., the assumption that the structure of within-species variation will be similar to the structure of between-species variation; as long as researchers are aware this assumption may not hold in any particular case. Galipaud and Kokko (2020) agree with this a priori expectation of alignment. They provide useful guidance on when and when not to expect patterns of variation across species to be repeated within a species too, among individuals. These authors, however, caution against overreliance on conclusions of the current models of life history evolution across species, as these have often not incorporated real-world complexities that apply, not least, to humans (e.g., conflict between the sexes). These may change model dynamics and predictions.

A claim in evolutionary psychology is that life history theory ‘predicts’ coherent suites of life history traits, which can be aligned along a fast-slow continuum (for review, see Nettle & Frankenhuis, 2020). The papers in this issue show that this claim is in fact controversial among leading theoreticians in evolutionary biology and evolutionary

psychology. Only some formal models make this prediction, and those models have limited applicability to humans. Moreover, formal models of the evolution of the fast-slow continuum have typically focused on a limited number of life history traits (for review, see Mathot & Frankenhuis, 2018), rather than the broader suites of life history traits, cognition, and physiology hypothesized to exist in humans (Belsky, Steinberg, & Draper, 1991; Ellis, Figueredo, Brumbach, & Schlomer, 2009) and other animals (Réale et al., 2010; Sih & Del Giudice, 2012). In our view, this gap needs to be addressed. As Stearns and Rodrigues (2020; this issue) contend: “The fast-slow continuum is an observation of a pattern, not a prediction from a model”; “One might claim that it does not matter what stimulates a hypothesis if it leads to testable predictions and a research program that makes progress. The danger, however, is that when a research program is getting the right answers for the wrong reasons, it will be a house built on sand”.

André and Rousset (2020) claim that, in fact, there is a formal basis for expecting a fast-slow continuum among individuals. They argue that Williams' (1957) hypothesis – that higher extrinsic mortality should increase investment in fertility and reduces investment in survival (i.e., a faster life history strategy) – is correct; but not, as intuition has it, because individuals should reproduce early and often before they die. In general, extrinsic mortality does not *directly* affect the evolution of life history traits. It only affects those traits *indirectly* through its effect on the intensity of competition (a form of density-dependence). Extrinsic mortality reduces competition. Fewer competitors increases the benefits of reproducing earlier and more often; for instance, because organisms and their offspring need to invest less in embodied capital (e.g., size) to be able to compete successfully. This result is well-established in evolutionary biology and needs to be better incorporated into the human literature.

André and Rousset (2020) argue that higher extrinsic mortality favors faster life histories not only between species and populations, via selection on genes, but also among individuals, as a facultative developmental response. As noted, they reject the argument that theoretical results from models exploring optimal life histories in stable environments cannot be generalized to variable environments (Baldini, 2015). This disagreement relates in part to the way in which the term ‘extrinsic mortality’ is defined and formalized (see also Del Giudice, this issue; Day & Abrams, 2020; Moorad, Promislow, & Silvertown, 2019). André and Rousset (2020) also argue that, contrary to claims in the human literature, it is not extrinsic mortality that drives life-history variation between harsh and supportive environments, but rather the tradeoff between mortality and fertility. These authors, therefore, would encourage future research in the existing tradition from evolutionary anthropology that quantifies this tradeoff across diverse human populations (for review, see Del Giudice, Gangestad, & Kaplan, 2015; Lawson & Bergerhoff Mulder, 2016; Bribiescas, 2020; see also the sections “Demonstrating trade-offs in humans” in Bolund, 2020 and “Life history research in evolutionary anthropology” in Sear, 2020).

In our view, this example illustrates a broader issue: life history research in psychology has become increasingly disconnected from life history theory in biology (for a bibliometric analysis, see Nettle & Frankenhuis, 2019). Many applications of life history theory in psychology are not straightforward extensions of life history research in evolutionary biology. Evolutionary biologists use the term ‘life history theory’ to refer to formal (i.e. mathematically explicit) models and the predictions deduced from them. Evolutionary psychologists often use the term to refer to a specific set of ideas that is largely independent from modeling and induced based on empirical observation (Nettle & Frankenhuis, 2019). Researchers can disagree on the value of formal modeling; and, there might even be benefits to the two bodies of research developing separately: one more deductive, the other more inductive. However, in that case, we need to be clear that this is the way we are choosing to move forward, and possibly use different names for the two approaches. For instance, if we infer that a trait (e.g., impulsivity) is ‘fast’ based on its correlation with other ‘fast’ traits (e.g.,

early reproduction), then it is potentially misleading to say that this association is ‘predicted’ by life history theory, since such a claim made in other areas of biology would imply that the prediction was an outcome of a formal model. In our own work, we use the term LHT-E to refer to the core research program in evolutionary biology, and LHT-P to refer to the core research program in psychology (Nettle & Frankenhuis, 2020). In the special issue, Sear (2020) has adopted this terminology as well.

Should life history research in psychology be firmly anchored to life history modeling from evolutionary biology, or do we accept looser ties? Our preference is for these bodies of research to grow closer together again, while recognizing that life history research can benefit from deductive as well as inductive approaches (see Barrett, 2020), as long as they are clearly distinguished. The papers in this issue identify clear gaps between life history research in psychology and mathematically informed models within biology, and outline directions for closing these gaps. We now turn to related empirical debates.

5. Do the data support a fast-slow continuum?

Our contributors agree that fast-slow continua can explain some of the variation in life histories among groups of organisms; i.e., across species or populations of mammals (including primates), birds, fish, reptiles, and insects (see references in Del Giudice, 2020). However, they disagree over how much variation is explained by these continua. For some group comparisons, estimates cover a rather large range, depending on which dataset is used and whether analyses control for such factors as body size and phylogeny. Indeed, whether or not to control for such factors is actually debated (e.g., because body size may itself be part of a life history strategy). Stearns and Rodrigues (2020, this issue) conclude: “much of the variation captured by the fast-slow idea resides at the level of differences among higher taxonomic units, not at the level of individual responses. The closer one approaches the individual level, the weaker the pattern becomes”. By contrast, Del Giudice (2020, this issue) argues that fast-slow continua are robust across different datasets and taxonomic levels. He also notes: “The notion that body size has a major impact on the nature of the fast-slow continuum is largely based on the studies by Bielby et al. (2007) and Jeschke and Kokko (2009); it is a misconception because, in both cases, the conclusions of the study are not supported by the data” (Del Giudice re-analyzes the data of these studies in his supplement). We offer that fast-slow continua in group comparisons are perhaps less strong and consistent than they are often depicted in the human literature.

There is less consensus about fast-slow continua among individuals both in humans and other animals. Some contributors argue there is no evidence, or only weak evidence, for a fast-slow continuum of individual differences in humans (Zietsch & Sidari, 2019). Others argue that the majority of data has been sampled from a very limited slice of the human species, and that more representative sampling actually reveals different patterns in different human populations (Sear, 2020). Other contributors present a new meta-analysis to address the mixed findings of previous research (Wu, Guo, Gao, & Kou, 2020).

A related claim to the fast-slow continuum is that early-life stress is also associated with individuals' faster or slower strategies revealed in risk, time, and prosocial preferences. Sear (2020) argues that, to date, there is limited theoretical justification for including a broad range of preferences and behaviors in the definition of a ‘life history strategy’. Life history strategies in biology typically refer to correlations between the life history traits of growth, reproduction and survival, not preferences and behaviors. Life history theory may certainly be useful in helping inform our understanding of preferences and behavioral traits, and has been successfully used in work on both human and non-human species exploring risk-taking behavior and present orientation (e.g., Wolf, Van Doorn, Leimar, & Weissing, 2007; for commentary, see McElreath, Luttbeg, Fogarty, Brodin, & Sih, 2007; for review, see Mathot & Frankenhuis, 2018). However, the little empirical work that

has tested whether life history traits are associated in consistent ways with preferences and behavioral traits has not always found the expected associations. To quantify this evidence, the special issue includes a meta-analysis.

The meta-analysis of Wu et al. (2020) shows that early-life stress is associated with more risk taking, greater present-orientation, and less prosociality, and its positive association with present-orientation is stronger in currently stressful situations. However, the overall effect sizes are small and a cautious interpretation of these findings is warranted by the variation in the results across different preference measures and some evidence of publication bias. Further, the meta-analysis is largely based on data from western high-income countries, and so it is an open question to what extent the results generalize to a broader spectrum of humanity. A recent meta-analysis of non-human animals found either very weak or no support at all for a fast-slow continuum of individual differences when analyzing the associations between life history traits and physiological traits (Royauté, Berdal, Garrison, & Dochtermann, 2018). Overall, the evidence base for coherent suites of life history traits including cognition and physiology, aligned along a fast-slow continuum, is limited in humans and other animals.

6. Limitations of human life history research

Empirical work in human life history faces three broad limitations. First, the tradeoffs thought to underlie the fast-slow continuum (e.g., current versus future reproduction, quality versus quantity of offspring) are often assumed, rather than tested (for exceptions, see references in Sear, 2020, the section “Life history research in evolutionary anthropology”). This is understandable, because tradeoffs are notoriously difficult to document empirically (Bolund, 2020). This limitation implies the need to properly calibrate and communicate our uncertainty about the tradeoffs we assume. This does not happen enough. Biologists have made many efforts to measure tradeoffs; however, they often did not find them in the places where they expected them (Metcalf, 2016; Roff & Fairbairn, 2007). Bolund (2020) discusses the challenges of measuring tradeoffs, including the conclusions that different study designs afford. Psychologists can benefit greatly from the lessons that biologists have learned over decades of research. These lessons include the difficulty or impossibility of demonstrating tradeoffs using between-subjects designs – for instance, individuals differ in overall quality, and therefore have different resource budgets to expend – and the benefits of using experimental or longitudinal within-subjects designs. Bolund illustrates these and other points using empirical research in diverse species. On the positive side, Bolund also discusses promising affordances for human life history research, such as the possibility of combining very large datasets of behavioral and life history observations with quantitative genetic methods.

Second, limited attention is paid to alternative explanations of the observed trait covariations, let alone presentation of the data needed to rule these explanations out (Stearns & Rodrigues, 2020; Zietsch & Sidari, 2019). For instance, few studies control for genetic confounding, and when studies do, associations between exposure to psychosocial stress and pace of life history frequently become weaker or null (see references in Barbaro, Boutwell, Barnes, & Shackelford, 2017; Zietsch & Sidari, 2019). On the other hand, psychosocial factors do explain a substantial portion of the remaining variance in some studies (e.g., Tither & Ellis, 2008). Overall, the empirical basis for a fast-slow continuum resulting from developmental plasticity may be weaker than it is often portrayed in the literature. Nonetheless, there is evidence, including the meta-analysis presented by Wu et al. (2020) in this issue, which suggests that this line of research captures some real-world variation. On the whole, we hope that human life history research will become more transparent about its assumptions and limitations. This will help to calibrate uncertainty and highlight gaps in the literature, which may inspire future research.

Third, there is ambiguity in the language used to describe

‘environmental unpredictability’ – which is thought to be a key factor in regulating human life history development – and in the proximate mechanisms that evolved to detect it. Young, Frankenhuis, and Ellis (2020) argue that these ambiguities obfuscate the logic from theory to prediction and raise questions about the measures that are currently used. To address conceptual ambiguity, Young et al. (2020) argue that environmental unpredictability might have different characteristics, depending on its precise statistical definition. For instance, current research on human life history does not explicitly address whether unpredictability is *stationary* or *non-stationary*. Stationarity refers to whether the statistical properties of an environment (e.g., mean, variance, autocorrelation) are constant or change over time (Frankenhuis, Panchanathan, & Nettle, 2016). However, change or stability in the mean, variance, or autocorrelation may pose different selection pressures and hence favor different adaptive strategies. To address ambiguity in mechanisms, Young et al. (2020) propose that organisms might ‘estimate’ (not necessarily consciously) environmental unpredictability in two distinct ways. The first is through exposure to specific cues (e.g., residential changes, loss of a parent) thought to correlate with unpredictability over evolutionary time. The second is through accumulation of lived experiences. Specifically, organisms may develop expectations about the world and respond adaptively to persistent violations of these expectations (i.e., prediction errors). Testing these hypotheses requires different types of measures. For instance, should empirical work count cues, such as residential changes (as is currently done), or quantify the statistical properties of lived experiences in time series data (as is often done in ecology and evolution, when such dimensions as rainfall, food availability, or social status are used to predict life history strategies) (for discussion of such data, see Frankenhuis, Nettle, & Dall, 2019)?

7. Conclusion

In a report of a workshop titled ‘Evolutionary life history analysis of human behavior’, published in 1983 in this journal – then called *Ethology and Sociobiology* – Weigel and Blurton Jones, 1983 concluded that: “detailed attention needs to be focused on theoretical developments before empirical endeavors can be said to ‘test’ whether human life history strategies are evolutionarily adaptive” (p. 235). Nearly 40 years later, we conclude that although there has been progress, the field has only partially fulfilled its promise. As Del Giudice notes in this issue: “the field needs to update its theoretical assumptions, rethink some methodological practices, and explore new approaches and ideas in light of the specific features of the human ecology”.

For some authors, the term ‘life history theory’ has narrowed to specific expectations about (some combination of) fast-slow continua, environmental harshness, and early-life stress. But life history theory is a much larger enterprise than any of these topics. It is a whole, changing branch of biology that studies how organisms allocate their limited resources (e.g., time, energy) across different fitness-relevant activities, such as growth, maintenance, and reproduction. It is a broad framework for studying questions; not a specific set of predictions. The framework affords building specific models, and these specific models make predictions. The framework itself, except in the very broadest sense, does not. As Stearns and Rodrigues (2020) put it: “Life history theory is an overarching set of ideas, an organizational paradigm, about what questions to ask, what assumptions to make, and what simplifications to accept. Within it, specific models can make different predictions about the responses to selection of population mean values of traits and of the plastic responses elicited as individuals develop from birth to adult to old age in interaction with their environments” (Stearns & Rodrigues, 2020, this issue).

The tremendous boost in human life history research of the past decade has brought valuable theoretical and methodological debates. Perhaps though, as Barrett (2020) has argued for the evolutionary human sciences more generally, we need to take stock of whether we

have settled too early and too rigidly on particular topics of study, things to measure, and sets of theoretical expectations. The time is ripe to pause and reflect on future directions for the field. This special issue discusses a selection of these debates from diverse viewpoints. We hope you will enjoy. It was a pleasure and honor for us to partake in this adventure.

Declaration of Competing Interest

None.

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