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How might life history theory contribute to life course theory?

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Commentary on the Theory Articles

In this commentary, we consider how evolutionary biology's *life history theory* (LHT) can be integrated with life course theorizing, to the benefit of both endeavors. We highlight areas where it can add value to existing work in life course theory (LCT), focusing on: how it can add an extra level of explanation, which may be helpful in understanding why individuals focus on their own health and happiness (or why they don't); how insights from comparative work, both across species and across all kinds of human populations, can inform LCT; and how social and biological researchers can come together fruitfully to make progress on the tricky issue of understanding human agency.

Life History Theory

LHT is a theoretical framework which considers how resources are allocated over an individual's life course, or 'life history' (Hill & Kaplan, 1999; Wells et al., 2017). Within LHT, resources can be invested in (1) growth, (2) maintenance (investment in one's health and survival), and (3) reproduction. Resources allocated to one function cannot be devoted to any other function. Central to life history theory is the *interdependence* between these domains, which leads to trade-offs: investing resources in one domain comes at the cost of not being able to invest these same resources in the other domains. These trade-offs are assumed to be resolved in ways that maximize the individual's fitness (i.e., genetic representation in future generations), with different ecologies leading to different resolutions. For example, a harsh environment with high mortality rates favors rapid growth and early reproduction, because postponing the onset of reproduction is risky when the chances of early death are high (Nettle, 2011). Similarly, more favorable environments typically allow for longer periods of growth and later ages at maturity, because investments in the body (in terms of maintenance, size, and learned skills) have higher fitness pay-offs later in life.

If we connect life history theory directly to the concepts of the *life course cube* developed in the article by Bernardi, Huinink, and Settersten (2018, p. 10), the similarities are striking. The *domains*—growth, maintenance, and reproduction—and their *interdependence* are key within life history. Similarly, *time-related interdependence* is at the core of life history theory. Investments in maintenance and growth in early life, which are possible because no resources are being diverted to reproduction before maturity, will have a positive impact on subsequent survival and lifespan, while an early start to reproduction will come at the cost of growth and subsequent survival. Path dependency, therefore, is central to the evolutionary life course literature, as evidenced by the large body of research on how early life experiences influence important life events (Ellis, 2004; Nettle, 2011).

With respect to the *multilevel interdependence* of the life course cube, the distinctions made between the *inner-individual level* (e.g., genes, physiology, preferences), the *individual level* (e.g., individual variation in health and wealth), and the *supra-individual level* (including the external environment and other individuals) are also useful distinctions within LHT. There is significant interest in *inner-individual* and *individual level* explanations of behavior, including studies of physiological differences between individuals, evolved predispositions and heuristics, and social learning effects.

However, an evolutionary perspective has far more to offer than simply acknowledging that genes matter or that some traits are rather fixed: the *supra-individual level* is also central to LHT, in that features of the environments in which the individual finds itself determine how energetic trade-offs are resolved and thus how behavior is shaped. A major distinction between the evolutionary and the social sciences can be found in the use of the supra-individual level, where social institutions (as exemplified by the article by Heckhausen and Buchmann, 2018) are given much less prominence in LHT. Instead, LHT emphasizes that individuals will respond to ecological aspects of the environment (e.g., mortality, resource availability), rather than just societal organization (Nettle et al., 2010; Virgo & Sear, 2016). Evolutionary scientists have further tended to focus on *meso-level* factors, such as immediate social relationships. There is considerable evolutionary research on family relationships, cooperation beyond the family, and sexual strategies; these factors are well known within the social sciences but almost seem lost in the life course cube. The article by Bidart (2018) similarly highlights the importance of such relationships in understanding the life course.

Ultimate and Proximate Explanations

LHT might be useful for life course theorizing because it allows different types of questions to be asked, a number of which are rarely considered within the social sciences. Within evolutionary theory, distinctions are made between so-called *ultimate* and *proximate*

explanations for why a particular behavior occurs (Mayr, 1961; Tinbergen, 1963). Ultimate explanations address why a particular behavior has evolved or why it is advantageous in terms of fitness. Proximate explanations consider how the behavior arises as a response to immediate factors in the environment. Thus, we could respond to the question "why do we eat?" in two ways: because our internal physiology sends (unpleasant) signals making us aware it is time to eat (proximate explanation) and also because if we didn't eat we would die, and that would reduce our fitness (ultimate explanation). Ultimate and proximate explanations co-exist at different levels of explanation, and each can be asked in the absence of the other. Yet, a full explanation of behavior requires understanding both ultimate and proximate causes of behavior (Tinbergen 1963).

The social sciences typically seek proximate explanations of behavior, so that ultimate explanations are not given much attention; particular behaviors or preferences are taken as "a given", rather than requiring explanation. For example, Bernardi and colleagues write that the "axiomatic assumption of a behavioral theory of the life course" is that "actors try to improve, or at least maintain, aspects of their physical and mental wellbeing" (p. 7). We agree with this assumption but would add that a complete life course theory would also address *why* individuals "tend to their wellbeing" (p. 4). An ultimate evolutionary explanation suggests that behaviors have evolved in such a way that they contribute to evolutionary fitness; behaviors that are fitness-enhancing will probably be those that an animal enjoys more than those behaviors that decrease fitness. Seen in this light, the assumption of welfare production in LCT is not much different from the assumption of maximizing fitness in LHT.

What if Welfare is Not Produced?

The life history perspective may also pay dividends when individuals do not seem to be striving for their welfare. Indeed, while wellbeing and evolutionary fitness may often align, it is clear that evolution does not produce individuals that maximize health and happiness, but

those that maximize fitness (Wells et al., 2017). For example, a disadvantaged socioeconomic position tends to be associated with behaviors that do not appear to maximize health, such as poorer diet, lower activity, smoking and drug use, and higher rates of teenage pregnancy (Pepper & Nettle, 2017). Yet when we take the perspective of life history theory, we could interpret such decisions as potentially adaptive in their particular environment: why adopt behaviors that only bring returns in the long-run, when one is relatively unlikely to live a long and prosperous life? A holistic, multi-level life course perspective, which includes acknowledgement that we are ultimately designed to maximize fitness, rather than health, wealth or happiness, should prove beneficial by helping prevent unintended consequences arising from well-intentioned attempts to improve human lives (Pepper & Nettle, 2017).

Looking Beyond the West

LHT is a framework that is generalizable across all different kinds of species, as well as human populations. This constitutes another advantage of this perspective. A comparative perspective across human populations (over both time and space) can help us understand which features of the human life course are relatively invariant and which respond most flexibly to the environment. Sociology, including life course research, already has a strong tradition of comparative research, but this tends to be confined to comparisons across industrialized nations. Evolutionary researchers, in contrast, roam around the globe and have a strong tradition of research in small-scale societies, as well as using historical data. While this volume takes an impressively interdisciplinary stance, anthropology is somewhat missing from its pages. Taking an anthropological and historical perspective illustrates just how contingent many life course behaviors are. For example, marriage and family formation, along with gender roles, vary considerably across societies. The sociological perspective, which holds that divorce and family complexity have increased recently and that 'male-breadwinning' has decreased (Bernardi et al., 2019, p. 16), only really holds for industrialized

nations since the Second World War, given that the male-breadwinner nuclear family has not been a common family form in human history (Fortunato, 2017; Sear, 2016).

Human Agency

Human agency is perhaps the elephant in the room in evolutionary theorizing. Life history theorists largely ignore agency. This should not be taken to mean that evolutionary scholars believe that agency does not exist or that all of behavior is genetically or biologically determined. Rather, the neglect of agency probably has more to do with the fact that acknowledging its existence would not improve evolutionary predictions: if life history theorists think about agency at all, it is probably as a proximate mechanism which generates behavior, and ultimate, evolutionary predictions are agnostic about mechanism. Nonetheless, ignoring its existence is one reason why the evolutionary and social sciences are still mostly separate disciplines (Smith, 2013).

At the same time, it is clear from the articles by Bernardi et al., Bidart, and Hechhausen and Buchmann that agency is a difficult topic and hard-to-define concept. While evolutionary theorists would be comfortable with the definition of agency put forward by Bernardi and colleagues (i.e., "individuals construct their own life course through the choices and actions they take within the opportunities and constraints of history and social circumstances," p. 8), they probably would feel less enthusiastic about Heckhausen and Buchmann's goal-focused "motivational framework," in which agency is defined as "individuals make decisions about which goals to engage with and which to disengage from" (p. 7). In short, life history theorists are likely to be happier with definitions of agency that do not have a strong focus on conscious deliberation. It is clear from introspection, after all, that we do not think explicitly in terms of fitness costs and benefits when making choices. Conscious thought may be more about a post-hoc rationalization of one's decisions, rather

than a consistently motivating force. Evolutionary theorists, then, tend to identify with John Lennon's words: "Life is what happens to you while you're busy making other plans."

Cross-species comparative work and evolutionary approaches may help in thinking about constraints on agency. As an example: a larger body size is strongly associated with reduced fertility rates across species, because body size is strongly linked to the amount of energy that individuals can harness from the environment, and higher energy use is (perhaps counter-intuitively) associated with lower fertility. Industrial human energy budgets are not constrained by body size, because we harness energy from extra-somatic recourses (e.g. from fossil fuels and nuclear power); the amount of energy people use in industrialized populations is equivalent to the predicted energy use of primates of 30,000 kg (Burnside et al., 2012). Strikingly, the fertility rate in such populations is exactly what one would predict for such a gigantic primate. This link between energy use and fertility rate holds across species, across primates, across human populations, and across industrialized populations. This certainly provides a novel perspective to low fertility in contemporary populations; such work might help reinforce the idea that—even when we think the behaviors arise due to conscious strategizing—this might not be the case.

Provocatively, then, a life history theorist might ask what value conscious deliberation adds to life course theorizing? If we observe that particular social institutions lead to more variation in behavior and choices (and agency is considered the cause), how would the concept of agency help in predicting behaviors, interdependencies, and so on? Equally provocative, for LHT practitioners, might be to ask how their models might change if they acknowledged that conscious deliberation could be an important determinant of human behavior, perhaps even an alternative level of explanation (Smith, 2013). It is clear that humans do engage in a considerable amount of introspection, so how would evolutionary models change if we accepted that both conscious and unconscious decision-making

(Kahneman, 2012) influences human choices? The concept of agency, while slippery, might well be an arena within which evolutionary and social scientists could engage in fruitful debate, in order to make genuine progress in understanding one another better; something that is necessary if we are to develop the truly interdisciplinary models required to understand our species.

Conclusion

The real question here, of course, is: what do we want from our theories and frameworks? Bidart writes aptly that the major challenge in understanding humans is "how to account for the multiple processes that combine in individuals as they live their lives…and how to explain them without crushing their complexity." Although Bidart provides convincing evidence for the central tenets of the life course cube and the interdependencies between domains and over time, she also shows that idiosyncrasies shape life courses and argues that unpredictability needs to be incorporated into life course theory. It is unlikely that a useful theory can be formed that is both predictive and incorporates such uncertainties, when addressing something so complex and open-ended as human lives. In our opinion, Bernardi and colleagues do the next best thing: they synthesize life course research from many disciplines and try to fit this research under one umbrella, providing us an excellent tool to study the life course.

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