Do human 'life history strategies' exist?

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Abstract

Interest in incorporating life history research from evolutionary biology into the human sciences has grown rapidly in recent years. Two core features of this research have the potential to prove valuable in strengthening theoretical frameworks in the health and social sciences: the idea that there is a fundamental trade-off between reproduction and health; and that environmental influences are important in determining how life histories develop. However, the literature on human life histories has increasingly travelled away from its origins in biology, and become conceptually diverse. For example, there are differences of opinion between evolutionary researchers about the extent to which behavioural traits associate with life history traits to form 'life history strategies'. Here, I review the different approaches to human life histories from evolutionary anthropologists, developmental psychologists and personality psychologists, in order to assess the evidence for human 'life history strategies'. While there is precedent in biology for the argument that some behavioural traits, notably risk-taking behaviour, may be linked in predictable ways with life history traits, there is little theoretical or empirical justification for including a very wide range of behavioural traits in a 'life history strategy'. Given the potential of life history approaches to provide a powerful theoretical framework for understanding human health and behaviour, I then recommend productive ways forward for the field: 1) greater focus on the life history trade-offs which underlie proposed strategies; 2) greater precision when using the language of life history theory and life history strategies; 3) collecting more empirical data, from a diverse range of populations, on linkages between life history traits, behavioural traits and the environment, including the underlying mechanisms which generate these linkages; and 4) greater integration with the social and health sciences.

Key words:

Life history research, fast-slow continuum, reproduction, survival, trade-offs, risk-taking behaviour, environment

Introduction

What is life history theory?

In evolutionary biology, love doesn’t so much hurt as kill: at the heart of life history research lies the assumption of a trade-off between reproduction and survival (Fisher, 1930; Roff, 1992; Stearns, 1992). Individuals are not ‘Darwinian demons’ able to devote unlimited energy to maximising both reproduction and survival at once (Law, 1979), but must make decisions about how best to allocate the limited resources they have access to. Those who invest heavily in reproduction will have fewer resources to spend on maintaining their own health and wellbeing, and so will have shorter lifespans.

Life history research is also about time. It’s concerned with how individuals solve the problem of allocating their energetic resources over their entire lifetimes. A slightly different way of formulating the trade-off between reproduction and survival is to frame it as a trade-off between current and future reproduction. Investing heavily in reproduction right now will involve costs, including the depletion of resources, meaning that fewer resources will be available for reproduction in the future (and the most extreme cost will be death, which definitely curtails reproduction).

‘Life history theory’ is a body of research in evolutionary biology focusing on how energy is allocated across the life course between the life history traits of growth, survival and reproduction, and how these are timed across the lifespan; incorporating research on growth rate, age at reproductive maturity, reproductive rate, number of offspring and age at death (Charnov, 1993; Roff, 1992; Stearns, 1989, 1992). This field is anchored in the assumption that there will be trade-offs between these traits, such as between reproduction and survival, current and future reproduction, and also between growth and reproduction. How features of the environment influence life histories is also a fundamental part of this research programme (Roff, 2002; Stearns, 2000).

‘Life history theory’ in the evolutionary social sciences

The above description, however, may not sound familiar to some evolutionary social scientists, or at least sound incomplete. In some areas of evolutionary psychology, ‘life history theory’ is now used synonymously with the idea of ‘life history strategies’. This research is inspired by work in evolutionary biology which observed that species can be lined up along a continuum of life history strategies, from ‘fast’ life history strategists who prioritise current reproduction over future reproduction, to ‘slow’ life history strategists, who invest more in growth and maintaining health (Promislow & Harvey, 1990). Fast life history strategists grow quickly, reproduce early and often, but at the cost of rapid senescence and early death (think of the mouse). Slow life history strategists grow slowly, reproduce late and rarely, and die at old ages (think of the elephant). This ‘fast-slow’ concept has been transferred from explaining differences between species to explaining differences between individuals in the evolutionary social sciences. In some versions of this approach, the concept of a ‘life history strategy’ has also been expanded to include several behavioural and psychological traits (B. J. Ellis, Figueredo, Brumbach, & Schlomer, 2009).

As life history research has been incorporated into the evolutionary social sciences, a number of conceptual differences have arisen between ‘life history’ research programmes in evolutionary biology and the evolutionary social sciences (Nettle & Frankenhuis, 2020). In a recent bibliographic analysis of life history research, Nettle and Frankenhuis (2019) demonstrated that LHT-E (their term for research using life history theory in evolutionary biology) and LHT-P (life history research in psychology) largely operate independently of one another, in that citations within these two literatures rarely overlap. The terminology used within each literature, however, is that of ‘life history theory': the use of the same terminology to refer to conceptually different research programmes has created a lot of confusion. To add to the confusion, the use of life history theory in the evolutionary social sciences is far from uniform; while some researchers work exclusively within the LHT-P paradigm, others draw more heavily on LHT-E to inform their work.

This paper aims to clear up some of this confusion in the literature on human life histories, by providing an overview of the different strands of this research in the evolutionary social sciences, with a particular focus on discussing the evidence for whether 'life history strategies' exist. Work on human life histories cannot be discussed without first a brief outline of some important take-home messages from LHT-E.

A brief historical overview of some important aspects of LHT-E

An important component of LHT-E involves investigation of how features of the environment affect life history traits and trade-offs. At the species level, environmental variation results in genotypes being shaped by natural selection, so that life histories become adapted to environmental conditions. At the individual level, environmental variation is assumed to affect life history traits through 'phenotypic plasticity': individuals can respond to environmental cues to shift their life histories adaptively. In other words, the same genotype can produce different phenotypes, or observable characteristics (Stearns & Koella, 1986; West-Eberhard, 2003). For example, age at puberty is influenced by access to good nutrition in childhood, and is earlier for well-nourished individuals (Kuzawa & Bragg, 2012). Note that this ability of a life history trait to respond adaptively to the environment is an evolved characteristic, even if the exact life history outcome for a particular individual is determined by environmental factors.

The earliest work on life history strategies suggested that unpredictable environments, in which mortality was 'density-independent', should favour species which exhibit a cluster of traits which result in rapid population growth (Pianka (1970), building on work by MacArthur and Wilson (1967) and Dobzhansky (1950)). Pianka suggested that an 'r-selected' strategy (using MacArthur & Wilson's r/K terminology) should involve many of the features of what became known as a 'fast life history strategy', in that reproduction happens early and often. In more stable environments where mortality was density-dependent and environments are saturated (i.e. cannot support rapid population growth) then 'K-selected' species are favoured, which exhibit traits characteristic of a slow life history strategy.

Population density and environmental saturation subsequently lost importance as environmental features which exerted selection pressures on species' life history strategies; instead, it was proposed that mortality risk in the environment could explain variation in life histories (Promislow & Harvey, 1990). In environments with high extrinsic mortality risk – where extrinsic mortality is defined as that beyond an individual's control – it was proposed that the best strategy is to grow fast and reproduce early and often, in order to produce offspring before an expected early death. Conversely, where extrinsic mortality rates are low, animals can afford to grow slowly and reach large size (which typically subsequently brings survival advantages), and reproduce late and rarely, since they can be more confident that a higher proportion of their offspring will survive into adulthood. That mortality risk should affect life history traits and strategies has become a prominent feature of work in the evolutionary social sciences, though this work assumes that mortality risk influences individual, not just species, differences in life histories (e.g. André & Rousset, 2020).

At the individual level, LHT-E is interested in the adaptive allocation of energy over the lifecourse between growth, maintaining one's own health (including immune defence) and reproductive effort.

This focus of interest means that it is not predominantly a behavioural discipline. Allocating reproductive effort does involve behavioural decisions – reproductive effort incorporates mating effort (including behaviours such as finding a mate), and parenting effort (including parenting behaviours) – but behavioural variation is not something the classic texts in LHT-E have paid much attention to (Roff, 1992; Stearns, 1976, 1992). In evolutionary biology, much of the work on mating and parental behaviour is done by behavioural ecologists – the branch of evolutionary biology interested in how behaviours vary adaptively across ecological contexts (Krebs & Davies, 1991; Nettle, Gibson, Lawson, & Sear, 2013). This discipline draws on LHT-E, but also on other evolutionary models which help explain behavioural variation.

Nevertheless, research on life histories is also about the *timing* of events across the life course, and this emphasis on time, particularly the emphasis on trade-offs between the present and the future, has led to the suggestion that life history traits may be correlated with one particular set of behaviours: those involving risk-taking. One line of argument has proposed that individuals for whom it is adaptive to invest in their health and longevity over current reproduction should be risk-averse, since such individuals have high future expectations and much to lose. Conversely, those for whom it's adaptive to invest in current reproduction because they lack an expectation of long, healthy life should be prone to take more risks, since they have little to lose. This reasoning has been used to suggest that certain types of animal personalities (risk-prone or risk-averse) may be adaptive, and should cluster together with certain life history traits at the individual level (Wolf, Van Doorn, Leimar, & Weissing, 2007). While this argument is not uncontroversial (McElreath, Luttbeg, Fogarty, Brodin, & Sih, 2007), it does mean that there is precedent in biology for assuming that certain behavioural traits may covary in predictable ways with life history traits between individuals. Note that this model is specific to risk-taking behaviour, however; other behaviours, cooperativeness for example, were not included in this model.

There is also a relatively new body of biological literature – encompassing our own and other species – suggesting that suites of traits, including some behavioural traits, cluster together at the individual level (Dammhahn, Dingemanse, Niemelä, & Réale, 2018; Réale et al., 2010). 'Pace of life syndrome' draws on LHT-E and work in the evolutionary social sciences to develop a model of within-species variation in the 'pace of life', which is similar to the 'fast-slow life history continuum'. But this model expands the range of traits included in the fast-slow continuum beyond life history traits to physiological characteristics, on the assumption that 'faster' life history strategies would be associated with particular physiological markers, such as higher metabolic rate, and to certain behavioural characteristics. These behaviours include aggression, dispersal behaviours and sociability, as well as risk-taking behaviours, but not mating strategy. While the popularity of this framework has been growing in biology, recent reviews have found relatively little support for this syndrome, either empirically (Royauté, Berdal, Garrison, & Dochtermann, 2018) or through formal modelling of the predicted covariation of different traits (Mathot & Frankenhuis, 2018).

To conclude this section: there are several important insights from LHT-E which can help us understand human health and behaviour, including the core assumptions that there will be trade-offs between life history traits; that life history traits and trade-offs will be affected by environmental variation; and that certain behaviours might be associated with life history traits. There is therefore considerable scope for LHT-E to make valuable contributions to the social and health sciences, but this requires that the current confusion in the literature clears sufficiently for those working both within and outside the evolutionary social sciences to navigate this research area easily.

Human life history research

There has been interest in applying life history research in biology to our species for decades: a workshop was held in 1983 on human life history research (Weigel & Blurton Jones, 1983). Over time, this research area has diverged into three branches, which fall along a continuum with varying degrees of closeness to LHT-E. These can be roughly divided into work done by evolutionary anthropologists (closest to LHT-E), evolutionary developmental psychologists, and evolutionary personality psychologists (LHT-P: the least similar to LHT-E). See Table 1 for a summary of similarities and differences between these three fields, and the biological literatures of LHT-E and pace of life syndrome.

There are a number of differences between these three lines of research, some of which relate to different foci of interest (involving the traits and populations under study), and which – with greater integration between fields – could be leveraged to generate an improved, more holistic understanding of human life histories. Evolutionary anthropology has focused on exploring trade-offs between the life history traits of growth, timing of maturation and first birth, fertility rate, incorporating into this research programme a limited range of behavioural variables, including parental investment and risk-taking behaviour; and investigations of how the environment shapes human life histories. Evolutionary developmental psychology is particularly interested in how early life experiences affect the development of reproductive strategies; their focus is mainly on behavioural traits, especially those relating to sexual behaviour and interpersonal relationships, though there has also been substantial interest in one life history trait - the timing of sexual maturation (puberty). Evolutionary personality psychologists are mostly interested in the 'fast-slow continuum of life history strategies', which in this research programme involves almost exclusively behavioural, rather than life history, traits.

There are significant conceptual differences between these three approaches, however, which will hamper progress, if not acknowledged and addressed. A key difference is in the way that 'life history strategies' are defined and used. Currently, the most popular approach to life histories in LHT-P involves measuring 'life history strategy' by using a battery of survey questions on a wide range of topics, none of which involve life history traits. This is typically referred to as the 'psychometric approach' to life history strategies. Collecting data on life history traits has been referred to as the 'biometric' or 'biodemographic' approach, in contrast (Black, Figueredo, & Jacobs, 2017; Figueredo et al., 2015). This terminology is rather unfortunate, as it gives the false impression that these are two approaches to studying the same underlying construct.

The 'psychometric' approach is designed to measure a fixed construct, the 'fast-slow continuum of life history strategy', which incorporates a range of behavioural, psychological and cognitive traits which are not considered part of a 'life history strategy' in biology or anthropology. All humans, both men and women, are assumed to lie somewhere on this single continuum of 'life history speed', and variation in life history speed is largely assumed to be genetically determined (Black et al., 2017; Figueredo, Vásquez, Brumbach, & Schneider, 2004). This construct is effectively a behavioural syndrome (Bergmüller, 2010), and so rather different from the conception of 'life history strategies' in evolutionary anthropology. Evolutionary anthropological research, rather than simply measuring the same concept of a 'fast-slow continuum' using the 'biometric' indicators of actual life history traits, instead is conceptually closer to LHT-E: it is more interested in understanding life history trade-offs, and in how environmental variation affects life history traits and trade-offs in different contexts. 'Life history strategies' will emerge from trade-offs, because trade-offs assume there are consistent linkages between traits, but life history strategies in evolutionary anthropology do not have the same fixed definition of a single universal fast-slow continuum. Evolutionary developmental psychology lies somewhere between the two approaches, closer to LHT-P in its focus on behaviour, but perhaps overall closer to evolutionary anthropology in its interest in how the environment influences the development of life histories, and acknowledgement of more flexibility in its definition of life history strategies.

The next section fleshes out differences and similarities between the three approaches, focusing particularly on the evolutionary anthropology approach as there are few recent reviews of this research area (but see e.g. Hill, 1993; Mace, 2000).

Life history research in evolutionary anthropology

Investigating life history trade-offs: Much early life history work in anthropology, drawing on LHT-E, focused on examining trade-offs between life history traits. A particularly thorough example is Hill and Hurtado's book *Ache Life History* (Hill & Hurtado, 1996). Hill and Hurtado brought together life history research in biology with the latest techniques and research in demography to inform their long-term ethnographic research among the Ache, a group of hunter-gatherers in South America. Hill and Hurtado explored several life history trade-offs both empirically, examining fertility, mortality and growth in this population, and with formal modelling. For example, they built a model of the 'optimal' age at first birth, which made predictions about the timing of the switch from growth to reproduction. This uses the 'optimality' approach (Parker & Maynard Smith, 1990) of biological life history research, which aims to find the predicted 'optimal' allocation of resources to different life history functions, which will maximise reproductive success. Hill and Hurtado found that the optimal age at first birth predicted by their model roughly corresponded to actual age at first birth for women in this population (see for further evidence of a trade-off between growth and reproduction: Allal, Sear, Prentice, & Mace, 2004; Sear, 2010).

Hill and Hurtado found less evidence in support for other predicted life history trade-offs. Looking for 'costs of reproduction' is one way of testing for trade-offs between current and future reproduction or survival using observational data. This involves investigating whether individuals who invest heavily in reproduction at one point in time suffer consequences at future time points in terms of lower survival or reproductive output. But in the Ache, early first births and high reproductive rates did not seem to have subsequent costs for future survival or fertility. Instead, early fertility seemed to be correlated with a higher reproductive rate in later life. This illustrates a significant problem with using observational data to look for life history trade-offs; sometimes known as the 'big car-big house' problem (or in biological jargon: 'phenotypic correlations' Van Noordwijk & De Jong, 1986). The assumption underlying life history trade-offs is that individuals have access to limited resources, so they must decide between investing in reproduction or survival, for example. But individuals with access to plentiful resources may be able to devote significant resources both to reproduction and survival, in the same way that wealthy people are able to afford both big cars and big houses (see Blolund, 2020 for more discussion of life history trade-offs).

Evolutionary biologists working with non-human species are able to experimentally manipulate their study organisms, allowing them to test life history hypotheses much more cleanly than is possible to do with observational data. To get around the problem that reproduction cannot be experimentally manipulated in our own species, sophisticated statistical techniques have been used on observational data instead. In statistical models, testing whether reproduction has a subsequent adverse impact on health (or survival) is confounded by the problem that good health leads to higher reproductive output. Techniques which are designed to account for this 'endogeneity' problem have had some success in demonstrating the predicted trade-off between reproduction and survival (Doblhammer & Oeppen, 2003). Research on the costs of reproduction is nevertheless somewhat inconclusive (Gurven et al., 2016; Lycett, Dunbar, & Voland, 2000; Penn & Smith, 2007; Sear, 2007).

One factor which may make finding costs of reproduction difficult in our species is that human mothers do not raise children alone, but make use of a 'pooled energy budget' (Kramer & Ellison, 2010; Reiches et al., 2009). In other words, mothers use the help of other family members to raise children (Hrdy, 2009), which may buffer them to some extent from experiencing costs of reproduction (Kramer, Greaves, & Ellison, 2009; Meehan, Quinlan, & Malcom, 2013). In addition, costs of reproduction may not be measured accurately if help from other relatives, such as grandmothering, is not incorporated into the measurements (Jasienska, 2009).

Evolutionary anthropologists have also been interested in trade-offs which involve parental effort, because of the considerable parental investment that human children need. In LHT-E, the trade-off between number and size of offspring has been examined: species tend to differ in either producing many small offspring, or fewer large offspring. This can be conceptualised as a trade-off between investing in the quality and quantity of offspring. Evolutionary anthropological research draws on this work in LHT-E, but is also informed by work on parental investment in other areas of evolutionary biology (e.g. Kokko & Jennions, 2008; Lack, 1954; Trivers, 1972). Hill and Hurtado were able to show some limited evidence for a quality-quantity trade-off in the Ache at the level of the individual child, in that short birth intervals were associated with slightly higher child mortality; but were not able to demonstrate clear evidence overall that women with high fertility had lower child survivorship (which might be expected if women traded off quantity against quality among their children).

The quality-quantity trade-off has been investigated in other populations with similarly mixed results (Borgerhoff Mulder, 1998; Lawson & Borgerhoff Mulder, 2016; Pennington & Harpending, 1993). Again, trade-offs are often only revealed when using sophisticated statistical techniques to deal with the problem of phenotypic correlations (Lawson, Alvergne, & Gibson, 2012; Strassmann & Gillespie, 2002). The quality-quantity trade-off has nevertheless featured in useful theoretical developments in evolutionary anthropology which have drawn on life history and parental investment theories to propose explanations for variation in human fertility, including explanations for how fertility changes with the shifts from hunting and gathering to agriculture, and agriculture to industrialisation (Kaplan, 1996; Kaplan & Lancaster, 2000; Kaplan, Lancaster, & Robson, 2003; Mace, 2000; Robson & Kaplan, 2005; Shenk, Kaplan, & Hooper, 2016; see also Wells & Stock, 2020).

Physiological mechanisms underlying life history trade-offs: there is a large body of research in anthropology which has explored the physiological mechanisms underlying life history trade-offs, and produced significant supporting evidence for some of these trade-offs (Ellison, 1990, 2017; Lancaster & Kaplan, 2009; Longman, Wells, & Stock, 2020; Vitzthum, 2008). The field of reproductive ecology has demonstrated that when energetic resources are scarce, women limit their reproductive capacity, in order to spare sufficient energy for maintaining health and survival (Ellison, 2003): both within and between populations, women who are less well-nourished or who have high energy expenditure have lower levels of reproductive hormones, indicating potentially lower reproductive capacity, than better-nourished women (Jasienska, 2003, 2011; Jasienska & Ellison, 1998; Vitzthum et al., 2002). Reproductive ecologists have also found evidence for the costs of reproduction in that reproductive effort is associated with subsequent oxidative damage, a marker of physiological stress (Ziomkiewicz et al., 2016).

This work on life history trade-offs suggests that drawing on LHT-E can be beneficial for understanding the human life course, by demonstrating evidence for life history trade-offs (particularly the work on physiological mechanisms). It also highlights some of the pitfalls in investigating these relationships (the problem of phenotypic correlations), as well as the most successful methods for doing so (a combination of formal modelling and empirical research).

Research on environmental influences on life history traits: mounting evidence suggests that variation in the environment is associated with variation in life history traits and trade-offs within our species. Some of this work has tested the hypothesis that higher mortality risk is associated with investing in reproduction over health, using the language of 'fast and slow' lives. This work is distinct from the LHT-P paradigm, however, in that it has focused on testing for associations between features of the environment and individual life history and related behavioural traits, rather than assuming a single, inherited continuum of 'life history strategy'. At the population level, this research has shown that higher mortality risk is associated with faster growth, and earlier puberty and first births for women across small-scale societies (Walker et al., 2006), and with earlier first births across nation-states (Low, Hazel, Parker, & Welch, 2008; Placek & Quinlan, 2012). But the predicted earlier and faster reproduction in high mortality settings is not always seen in population-level data, particularly for regions of the world where mortality has fluctuated recently (K. G. Anderson, 2010).

Within-population analysis has mainly used datasets from large, stratified, high income countries. Research on UK data has shown that in areas in which mortality risk is higher, average age at first birth is earlier and reproductive rate may be faster (Nettle, 2010, 2011; Uggla & Mace, 2016); younger women also have lower abortion rates, interpreted as evidence that younger women prioritise reproduction in high mortality environments (Virgo & Sear, 2016). Individual-level analysis has also found evidence that stressors experienced in early life, which may be proxies of mortality risk, are associated with an earlier start to reproduction and/or sexual activity, in the UK and in several other high income populations (Chisholm, Quinlivan, Petersen, & Coall, 2005; Clutterbuck, Adams, & Nettle, 2015; Coall, Tickner, McAllister, & Sheppard, 2016; Nettle, Coall, & Dickins, 2010b, 2010a; Snopkowski & Ziker, 2019). Rare examples of research which has investigated early life stressors and later life history traits in middle income contexts have also found some evidence that stress is associated with earlier sexual debut and first births, but also some notable differences from results in high income contexts (e.g. Richardson et al., 2020). In Brazil, for example, early life adversity was associated with a delayed, rather than accelerated menarche (Wells et al., 2019); and in Siberia, economic stress was not associated with an early start to reproduction (Nolin & Ziker, 2016).

Research on how the environment shapes life histories has also demonstrated that the early life environment can shift hormonal pathways, potentially mediating early life influences on later life history traits. Migration from a more, to a less, energetically stressed environment (Bangladesh to the UK) results in a dose-response shift in reproductive hormones: those who spend longer periods of their early life under energetic stress have progressively lower hormonal levels (Houghton et al., 2014; Núñez-de la Mora, Chatterton, Choudhury, Napolitano, & Bentley, 2007). LHT-E has also been used successfully in evolutionary anthropology to develop a better understanding of human growth, from foetal growth through to the pubertal transition (Ellison et al., 2012; Kuzawa & Bragg, 2012; Kuziez, Harkey, Burack, Borja, & Quinn, 2020; Lummaa, 2003; Martin & Valeggia, 2018; Rutherford et al., 2019; Wells, 2010); for example, by using the principle of life history trade-offs to understand why growth rates are reduced in adverse environments (Bogin, Silva, & Rios, 2007).

Environmental influences and behavioural traits: environmental influences on parental investment have also been investigated by evolutionary anthropologists (Quinlan & Quinlan, 2007). The assumption is that environments which shift individuals towards a focus on current reproduction, also result in investment in quantity over quality of offspring, reducing investment in each individual child (Promislow & Harvey, 1990). A caveat here is that some life history research suggests that there may be more than one axis of life history variation: for example, one which measures the timing of reproductive events (early births and rapid reproductive rate) and a separate axis which measures the trade-off between offspring size and quantity (Bielby et al., 2007; but see Del Giudice, 2020). Nevertheless, in the UK, lower parental investment as measured by breastfeeding initiation and duration, does seem to be associated with lower quality environments, suggesting it may cluster together with other traits which indicate an emphasis on current over future reproduction, such as early maturation and first births (L. J. Brown & Sear, 2017; Nettle, 2010).

Beyond parental behaviours, this line of research has also demonstrated considerable evidence that another type of behavioural variation is linked to mortality risk and stressful environments (Frankenhuis, Panchanathan, & Nettle, 2016; Nettle, 2015; Nettle et al., 2010b; Pepper & Nettle, 2014a, 2014c, 2014b): behaviours which may be linked to risk-taking behaviour, such as those which indicate ‘future discounting’ (a focus on the present rather than the future) and low perceived control over one’s environment (see also Uggla & Mace, 2015). This ‘behavioural constellation of deprivation’ (Pepper & Nettle, 2017) is akin to work in biology suggesting risk-taking behaviours may be linked to life histories which prioritise current over future reproduction (Wolf et al., 2007), though note that risk preference and time preference, though they may be related, are not quite the same thing (Anderhub, Güth, Gneezy, & Sonsino, 2001; Andreoni & Sprenger, 2012).

Evidence for a ‘fast-slow continuum’ of ‘life history strategy’? Some research on associations between the environment and life history traits has tested multiple life history or behavioural traits in the same study, which can speak to the question of whether traits hang together in clusters. This research suggests some evidence for clustering in women: for example, early life adversity is associated with earlier first births and earlier menarche, first sex, intended first births and more risk-taking behaviour (Nettle et al., 2010a; Sheppard, Garcia, & Sear, 2014; Sheppard, Schaffnit, Garcia, & Sear, 2014); and, in one study, higher total fertility (Sheppard, Pearce, & Sear, 2015). The evidence is weaker for clustering in men, in that some indicators of early life adversity are associated with delayed puberty, but earlier first births (Sheppard, Garcia, et al., 2014; Sheppard, Garcia, & Sear, 2015; Sheppard & Sear, 2012; Xu, Norton, & Rahman, 2018). These studies have mostly focused on life history and behavioural traits in a narrow age range, however, around adolescence and early adulthood, rather than the entire life course; and are mostly from English-speaking, high income countries. The few examples of similar work from middle income contexts, while also finding some limited evidence for clustering of traits, provide further evidence that a universal fast-slow continuum is unlikely to exist, given that the clustering looks a little different in such contexts (Richardson et al., 2020). In Brazil, for example, earlier first births, more risk-taking behaviour and some indicators of poorer health clustered together, but not earlier menarche (Wells et al., 2019).

Very recently, there has been a flurry of interest explicitly testing whether life history and related behavioural traits do hang together in coherent ‘fast-slow’ strategies, likely due to the popularity of this concept in LHT-P. This research has used a range of different methods, and found evidence for some clustering of traits, but not conclusive evidence for a single fast-slow continuum of life history. Mell and colleagues reported evidence that reproductive and health traits did cluster into ‘fast’ and ‘slow’ categories, using French survey data (Mell, Safra, Algan, Baumard, & Chevallier, 2018). In contrast, Brown and Sear added parenting traits to their analysis of reproductive and health traits in two UK samples, and found that, despite some evidence of the predicted clustering of traits, the ‘fast-slow’ continuum did not receive overwhelming support, not least because there was within-sample variation, in that clusters of traits looked different for White women and women of Pakistani origin (L. J. Brown & Sear, n.d.). Again using UK data, a Mendelian randomisation study found that menarche was associated with some later life history traits, such as first and last birth, but not others, such as risk-taking behaviour (Lawn et al., 2020). Two further studies, one using US data and one data from Serbia, found little evidence at all for clustering of life events (Sheppard & Van Winkle, 2020) or for the correlations between 'psychometric' and 'biometric' indicators predicted by LHT-P's 'fast-slow continuum' (Međedović, n.d.).

Life history research in evolutionary developmental psychology

Reflecting the interests of their discipline, evolutionary developmental psychologists have produced considerable research on how children's early life environment influences the development of reproductive strategies. Pushing back against the long-held assumption in psychology that early life adversity results in subsequent dysfunction, evolutionary developmental psychologists proposed in the 1990s that features of a child's early environment cause shifts in the development of life history and behavioural traits in order to produce adults who are best adapted to their environments (Belsky, Steinberg, & Draper, 1991). This 'evolutionary theory of socialisation' proposed that children who experience family stresses, including father absence, should experience early puberty, 'precocious' sexuality and anxiety (in women) or aggression (men), as such a strategy results in higher reproductive success in a stressful adult environment where paternal investment was likely to be low, and interpersonal relationships unreliable.

Life history research from biology was explicitly incorporated into later versions of this model, which considered father absence and other childhood stressors as indicators of mortality risk in the environment (Chisholm, 1993). This work has stimulated a large body of subsequent research which has produced considerable theoretical (Belsky, 2005; Del Giudice & Belsky, 2011; Del Giudice, Ellis, & Shirtcliff, 2011; B. J. Ellis, 2004; B. J. Ellis & Del Giudice, 2019) and empirical (Belsky, 2012; Coall et al., 2016; see for reviews: Webster, Graber, Gesselman, Crosier, & Schember, 2014) advances on how and why the early life environment should affect the development of certain life history traits and behaviours. Some of this research has focused on a proposed mechanism mediating early life environment and subsequent traits: 'attachment' and other measures of the relationship between parents and children in early childhood (Chisholm, 1999; Del Giudice, 2009; Hentges, Shaw, & Wang, 2018; Sturge-Apple, Davies, Martin, Cicchetti, & Hentges, 2012). Empirical research has been conducted almost entirely in high income countries, using both nationally representative surveys (Brumbach, Figueredo, & Ellis, 2009) and convenience samples of students (Kruger & Fisher, 2008), which are particularly useful for experimental studies (DelPriore, Proffitt Leyva, Ellis, & Hill, 2018).

Like evolutionary anthropologists, evolutionary developmental psychologists have largely focused on examining associations between the environment and individual life history and behavioural traits, based on the implicit assumption that certain trait will cluster together, rather than explicitly testing whether suites of life history and behavioural traits covary in predictable ways. The traits developmental psychologists have explored are somewhat different, though, and encompass a wider range of behavioural traits; relatively little research has been conducted on reproductive traits, such as age at first birth or total number of children. The timing of puberty is incorporated, however, as a key indicator of life history strategy (B. J. Ellis, 2004; Webster et al., 2014), as is the timing of first sex and number of sexual partners.

Sexual behaviour is of particular interest – initially because the anthropological research which originally inspired this work proposed that father absence in childhood should predispose girls towards a 'short -term mating strategy', which involves multiple short-term relationships (Draper & Harpending, 1982). Subsequently, interest in sexual behaviour developed a theoretical grounding in the assumed trade-off between mating effort and parenting effort. Fast life history strategists are considered to be those who invest in mating effort over parental effort, and so develop behaviours which best suit them to finding multiple mates; slow life history strategists are those who invest in parenting over mating effort, so develop affiliative behaviours which allow them to form successful long-term partnerships and invest heavily in their children (B. J. Ellis & Del Giudice, 2019).

While these ideas were not originally couched in 'fast-slow' language, evolutionary developmental psychologists developed over time an explicit interest in the fast-slow continuum of 'human life history strategies' (B. J. Ellis et al., 2009). Theoretical treatments of this research area use a relatively expansive definition of life history strategies, including both life history traits and behavioural traits related to parental investment and mating strategies. Such work also draws on LHT-E to recognise the many complexities in how life histories develop, acknowledging that the same life history and behavioural traits won't always cluster together in exactly the same way in all contexts. These complexities included highlighting how 'harshness' (high mortality rates) and unpredictability in the environment should have different influences on life history strategies, and their components; how juvenile and adult mortality risk are predicted to have different influences on life history strategy (see also Promislow & Harvey, 1990); and the importance of considering energetic constraints (see also Coall & Chisholm, 2003; Walker et al., 2006). Evolutionary developmental psychologists acknowledge that trade-offs between current and future reproduction, quantity versus quality of offspring and parenting versus mating effort are all distinct components of 'life history strategy'. Trade-offs between mating and parenting, therefore, are not inevitably tied to trade-offs regarding the timing of reproductive events. Nevertheless, these researchers suggest it is reasonable to consider them together given that these components often do covary in predictable ways (Del Giudice & Belsky, 2011).

The 'psychometric approach' in evolutionary personality psychology

This section focuses on the 'psychometric' literature in evolutionary personality psychology which uses life history language but which is conceptually the most distant from LHT-E; other work in evolutionary psychology inspired by LHT-E will not be covered here (e.g. Sng, Neuberg, Varnum, & Kenrick, 2017; Wilson & Daly, 1997). The 'psychometric approach' is exclusively interested in 'life history strategies' rather than individual traits (Black et al., 2017; Figueredo et al., 2015). The definition of life history strategies is much broader than that of other approaches, incorporating not just development, reproductive events, parenting and mating strategies, and risk-taking behaviour, but a host of other behavioural, cognitive and psychological variables (Figueredo, Vasquez, Brumbach, & Schneider, 2007). Further, empirical work in this area sometimes uses 'life history strategy' as the predictor variable, in order to determine how 'life history strategy' influences other behaviours (e.g. Salmon, Figueredo, & Woodburn, 2009). This likely stems from a significant difference between the psychometric and other approaches: in the former, life history strategies are assumed to be largely inherited, while other approaches assume that life history traits and strategies are plastic (within certain bounds), so there is considerable interest in how environmental factors affect this plasticity.

There are several different psychometric tools which have been used to measure life history strategy in this LHT-P paradigm, but the most commonly used is the Arizona Life History Battery (ALHB)[1], and its short form, the mini-K (Figueredo et al., 2017, 2007, 2006, 2005). The ALHB includes questions on 'insight, planning and control', 'mother/father relationship quality', 'family social contact and support', 'friends social contact and support', 'experiences in close relationships', 'general altruism' and 'religiosity', but no questions on life history traits. There are also no questions on the timing of

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[1] https://arizona.app.box.com/s/1prthk79i0zersjeqylgbrwwyfprju4y

life events, despite the intent of the tool to measure ‘life history speed’. While a few of these questions relate to behaviours which have been proposed to be associated with life history traits, such as risk-taking, most seem to have little to do with life history strategies if ‘life history’ is meant to be anchored in LHT-E. This may not matter if there was strong evidence that an individual’s position on this psychometric scale was associated with life history traits; the underlying assumption of psychometric approaches is that this battery of questions will reveal a latent variable, which is an indicator of an individual’s position on the ‘fast-slow’ continuum. Surprisingly little research has been conducted to test whether these psychometric measures do correlate with ‘biometric’ life history traits, but the few studies which have done so do not find the predicted associations (Copping, Campbell, & Muncer, 2014; Međedović, n.d.). In fact, three studies have now found that a slow life history strategy, as measured on a psychometric scale, was associated with higher fertility, rather than the lower fertility characteristic of a slow life history in LHT-E (Mathes, 2018; Međedović, n.d.; Woodley of Menie et al., 2017). This is perhaps because higher religiosity is included as a marker of a ‘slow life history strategy’ in these psychometric tools, yet greater religiosity is known to be associated with higher fertility (Zhang, 2008).

An illustration of some of the conceptual differences between LHT-P and LHT-E is the treatment of sex in the two paradigms (Copping & Richardson, 2020). Current psychometric approaches use the same measure of life history strategy for both sexes, and assume that males and females can be compared against one another in terms of ‘life history speed’ (Figueredo et al., 2015). In contrast, life history approaches in evolutionary biology, anthropology and developmental psychology analyse males and females separately, because of the recognition that the optimal solution to a particular life history problem may differ between the sexes (Del Giudice, 2009; Sheppard, Garcia, et al., 2015). The conclusion of the psychometric approach that men have ‘faster’ life history strategies than women (Figueredo et al., 2015) is therefore puzzling, especially given that women are ‘faster’ than men on key life history traits such as earlier age at maturation and first birth (see also: Tarka, Guenther, Niemelä, Nakagawa, & Noble, 2018).

Despite this disconnect between LHT-E and the psychometric approach, claims do appear that this approach is grounded in LHT-E, for example: *“Life History Theory predicts that many psychosocial traits will accumulate non-randomly”* (Figueredo et al., 2006). But LHT-E has little to say about psychosocial traits. Psychometric approaches, as currently applied, instead appear to descend conceptually from Rushton’s ‘differential K theory’ (Rushton, 1985, 1996). This model assumes that human races can be distinguished on a single, heritable, ‘K factor’ continuum, from (using Rushton’s terminology) ‘Negroid’ races at the ‘r-selected’ end of the spectrum, prioritising reproduction over health and mating effort over parenting effort; through ‘Caucasoid’ to ‘Mongoloid’ races at the opposite ‘K-selected’ end. This model used the biological language of ‘r/K selection theory’ (MacArthur & Wilson, 1967), but extrapolated far beyond the life history traits incorporated into the original r/K model to incorporate a whole suite of other characteristics, such as intelligence, altruism and genital size, for which little theoretical or empirical justification exists (multiple critiques have been made of Rushton’s work: Allen, Eriksson, Fellman, Poinsi, & Vandenberg, 1992; J. L. Anderson, 1991; Cain & Vanderwolf, 1990; Cernovsky, 1990; Lynn, 1989; Weizmann, Wiener, Wiesenthal, & Ziegler, 1990; Zuckerman & Brody, 1988) (not least because of the scientific consensus that race is not biologically meaningful: Benn Torres, 2019; Van Arsdale, 2019; Wagner et al., 2017).

The ‘fast-slow continuum’ paradigm in LHT-P does not focus on racial differences, but it does adopt key conceptual planks of differential-K theory (Black et al., 2017), none of which are particularly common in LHT-E (at least when explaining within-species variation): the ideas that a wide range of traits, including many behavioural and cognitive traits, cluster together with life history traits; that all humans can be lined up along a single dimension of variation 'life history strategy'; and that these individual differences are largely underpinned by genetic variation, rather than environmentally-induced plasticity.

The usefulness of the psychometric approach to 'life history strategy', or at least its current focus on the 'fast-slow continuum', has now been questioned on multiple grounds (see the special issue of the journal *Evolutionary Psychology* on "Psychometrics and Variation in Human Life History Indicators", 2017, for more detail on some of these critiques, with responses). There are theoretical concerns about whether the psychometric approach sufficiently distinguishes between proximate and ultimate explanations (Gruijters & Fleuren, 2018). Methodologically, the use of a single figure index to represent 'life history strategy' is considered highly problematic by some psychologists (Copping et al., 2014; Copping, Campbell, Muncer, & Richardson, 2017). The battery of questions used in the ALHB mixes up behaviours which might be associated with a life history strategy (such as risk-taking) with environmental influences which have been proposed to calibrate life history strategies (mother/father relationship quality), for example. Several studies have now shown these psychometric tools do not reflect well a single underlying latent variable (Manson, Chua, & Lukaszewski, 2020) but reflect several different independent dimensions of 'life history strategy' (Copping et al., 2014; Richardson, Dariotis, & Lai, 2017; Richardson, Sanning, et al., 2017).

If psychometric approaches are to prove helpful in understanding how and why behavioural and psychological traits are linked to life history traits, these approaches should investigate multiple different dimensions of 'life history strategy', such as the timing of life history events, the trade-off between mating and parenting, and between quality and quantity of offspring, rather than assuming there is only one dimension of 'life history speed'. Psychometric tools also need rigorous testing against life history and related behavioural traits, to provide evidence that they do reflect the construct they are designed to measure.

More broadly, there are concerns about applying the 'fast-slow continuum' to understanding differences between individuals regardless of whether or not psychometric tools are used, especially if multiple behavioural traits are incorporated into this vision of 'life history strategies'. A recent critique emphasised that transposing the 'fast-slow continuum' from between- to within-species research assumes that suites of traits respond to the environment similarly at both genetic and phenotypic levels, yet different processes determine responses at genetic versus phenotypic level (Zietsch & Sidari, 2019). One of the main architects of LHT-E, in this issue, has warned about the dangers of drawing analogies between species-level and individual-level variation in different sets of traits, without a thorough understanding of the causes of these traits and their correlations, and without formal modelling of the many assumptions that go into such verbal models (Stearns & Rodrigues, 2020).

Concerns about current applications of life history theory to the human sciences should addressed. The LHT-E framework is a powerful theoretical framework which has already helped inform research in the human sciences, and which has the potential to be far more widely used to understand human health and behaviour, if the field can move forward in a sufficiently rigorous way. Concrete suggestions for productive ways forward follow.

Ways forward

Greater emphasis on trade-offs, not strategies

More emphasis should be placed on understanding life history trade-offs (see Blolund, 2020 for examples of how to do this). Life history strategies arise because life history traits are correlated with one another, or trade-off against one another. Keeping sight of this will help keep life history research grounded in the core principles of LHT-E. Too much emphasis on strategies has introduced confusion into the literature, given that there is not a consistent definition of life history strategies in the evolutionary social sciences. The focus on strategies also runs the risk of developing quite a rigid view of life history strategies, which are assumed to look the same in all contexts. LHT-E was not intended to be the kind framework which can be used to generate predictions which will apply in all contexts, but to be a framework which can be used to generate specific predictions given a certain set of assumptions (Stearns, 1992).

The concept of the ‘fast-slow continuum’ of life history strategies needs to be used with particular caution. This has the potential to be a powerful heuristic informing research on human health and behaviour, given it is underpinned by the fundamental insight of a trade-off between reproduction and survival. But far more work needs to be done testing assumptions underlying this model. It also should be used as a heuristic, a guide to what human life histories might look like in different contexts, and not assumed to be an incontrovertible truth.

Greater clarity over terminology

Distinguishing between the paradigms of LHT-E and LHT-P in literature on human life history would help reduce terminological confusion, as would greater precision when using the term ‘life history strategies’. The same term is used to describe the LHT-P paradigm of a fixed ‘fast-slow continuum of life history speed’, as well the more flexible, sometimes domain-specific, life history strategies, discussed in the evolutionary anthropological and developmental psychology literatures. The latter definition enables a more nuanced, context-specific understanding of human life history traits and trade-offs. A key conclusion of this paper is not that human life history strategies do not exist, but that the term should be used carefully, and preferably not used to refer to strategies which encompass predominantly behavioural and cognitive traits. Greater integration with pace of life syndrome, including adopting its terminology, might be useful if a broad range of traits are to be included alongside life history traits as part of a ‘strategy’. Restricting the terminology of ‘life history’ traits exclusively to the life history traits of growth, reproductive traits, health and survival, rather than behavioural traits, would also introduce greater clarity into this literature. Greater precision should also be used when making claims about what ‘life history theory’ is and what it predicts. It is not simply a theory about the ‘fast-slow continuum’.

Improved understanding of how and why traits cluster, and how the environment influences clustering

More research is needed to understand (i) how and (ii) why life history traits and associated behavioural traits are linked together, and (i) how and (ii) why these are correlated with features of the environment. There is already very valuable work in this area, but progress is hampered by the tendency in the evolutionary social sciences to ‘theory-worship’ (Barrett, 2020). This means that particular theoretical frameworks quickly become solidified in the discipline, before these frameworks are rigorously tested, and then subsequent work becomes focused on finding empirical evidence to support this theory. Theory-worship is a particular problem if the theory being worshipped has weak foundations. Calls have been made elsewhere that more formal modelling is badly needed to strengthen the theoretical basis of research on human life histories, since this allows verbal arguments to be clearly specified and their assumptions tested (Frankenhuis & Tiokhin, 2018; Mathot & Frankenhuis, 2018; Nettle & Frankenhuis, 2019, 2020; Stearns & Rodrigues, 2020).

In additional to more formal theory, more descriptive empirical data, taking a more open-minded approach to life history trade-offs and strategies is also necessary to understand human life histories (Sear, 2020). Fruitful lines of enquiry would involve more integrated research on the proximate mechanisms, both physiological and psychological (McAllister, Pepper, Virgo, & Coall, 2016), as well as genetic influences (Barbaro, Boutwell, Barnes, & Shackelford, 2017; Mills, Barban, & Tropf, 2018), which link life history and associated behavioural traits to each other and to the environment.

More cross-cultural work

It is particularly important that this empirical data comes from a range of different contexts. While the work on life history trade-offs, and underlying physiological mechanisms, tends to come from small-scale societies in lower and middle income contexts, work linking behavioural and life history traits, and how the early environment influences them, comes predominantly from WEIRD contexts (Western, Educated, Industrialised, Rich and Democratic: Henrich, Heine, & Norenzayan, 2010) (Gettler, McDade, Bragg, Feranil, & Kuzawa, 2015; Kyweluk, Georgiev, Borja, Gettler, & Kuzawa, 2018). This is likely to lead to distortions in our understanding of human life histories, if different pieces of evidence needed to understand life histories come from different contexts.

Adaptive hypotheses, for example that high mortality risk in early life leads to earlier maturation and reproduction, need to be tested across multiple contexts to establish their cross-cultural validity, especially given the wide range of environments humans now occupy. Ultimately, the aim of applying LHT-E to the human sciences should be to understand variation in human life histories both within and between populations, by developing clear theoretical predictions which apply under a particular set of assumptions (such as about features of the environment), formally modelled and then tested empirically. We are not yet at that stage in the development of the discipline, so a first step may need to be relatively exploratory analysis which provides empirical evidence on whether particular hypotheses popular in the evolutionary social sciences hold up cross-culturally. For example, a common assumption in LHT-P is that father absence will be associated with earlier puberty in girls, but a recent review of literature on this topic found that, while this association is common in WEIRD samples, it does not hold up cross-culturally (Sear, Sheppard, & Coall, 2019).

Cross-cultural comparisons ultimately could be leveraged to better understand what human life histories look like; how variation in resource access affects life history traits; how different mortality regimes (for example, the ratio of juvenile to adult mortality) influence life history and related traits; how cooperative childrearing may affect life history trade-offs and strategies; and the influence of environmental features such as unpredictability and population density, and of cultural factors.

Greater integration with the social and health sciences

The social and health sciences have produced an enormous amount of relevant empirical data and theoretical work on aspects of human life history. Some examples: there is substantial work on how stresses associated with disadvantaged socioeconomic position become embodied to affect health (Geronimus, 1992; Geronimus et al., 2016; Vineis et al., 2020); the sociological field of life course analysis has produced considerable data on how reproductive and other life events are patterned across the lifespan (work which is now beginning to incorporate life history approaches: Bernardi, Huinink, & Settersten, 2019); the field of evolutionary demography has united LHT-E and demography to produce fascinating work on how life history traits such as age-specific fertility and mortality differ across species, which can help inform our own life history patterns (Jones et al., 2014), and which includes work demonstrating more than one axis of life history variation (Jones et al., n.d.).

Dialogue between evolutionary disciplines and other social and health sciences is also important because of the power of life history theory to generate insightful predictions, provided these predictions and underlying assumptions are thoroughly tested and applied in appropriate contexts. Such a powerful theoretical framework can add significant value to our understanding of real world problems, and inform interventions (Gibson & Mace, 2006). This has already been recognised by the emerging disciplines of evolutionary medicine (Alvergne, Jenkinson, & Faurie, 2016; Nesse & Williams, 1995), evolutionary public health (see e.g. the Lancet special issue on Evolutionary Public Health: Wells, Nesse, Sear, Johnstone, & Stearns, 2017) and applied evolutionary anthropology (Gibson & Lawson, 2014; Hill, 1993), but there is still considerable work to do before these ideas become mainstream in the social and health sciences.

Specific suggestions for topics to focus on in future research

Socioeconomic inequalities: some of the most valuable work using life history approaches in the evolutionary social sciences is that which draws on LHT-E and evolutionary developmental psychology to develop a better understanding of why socioeconomically disadvantaged groups have poorer health and shorter lifespans than advantaged groups. Understanding why such health inequalities exist is important if we are to develop interventions which have the potential to reduce these inequities (Nettle, 2015, 2019; Pepper & Nettle, 2014c, 2017). This work has highlighted, for example, that differences in life history traits and behaviour between disadvantaged and advantaged groups are not exclusively driven by ‘deficits’ in ability but by responses which are appropriate in particular environments (Frankenhuis & Nettle, 2020; Sheehy-Skeffington, 2020). Work in this area is sufficiently nuanced to provide a counterpoint to the assumption common in LHT-P that greater cooperativeness or altruism is associated with a ‘slow life history strategy’ (Figueredo et al., 2005). For example, poverty appears to result in a focus on ‘socially close’ rather than ‘socially distant’ individuals (Sheehy-Skeffington & Rea, 2017), which may be interpreted in some studies as a lack of cooperativeness, depending on how this trait is measured.

This research area has included a range of methods, including formal theorisation of its assumptions, but empirical analysis has largely come from high income countries (but see Alami, Stieglitz, Kaplan, & Gurven, 2018; Wells et al., 2019). Future work could usefully be directed at researching lower income contexts, to investigate whether the approach can achieve similar success in explaining health inequalities across a range of contexts.

Mating strategies: in psychological approaches to life history, a ‘fast’ life history strategy is one in which mating effort is prioritised over parenting effort (see for debate about whether such a trade-off exists: Stiver & Alonzo, 2009). This involves engaging in a ‘short-term’ mating strategy, with greater interest in sex and many short-term partnerships (see for discussion of short- and long-term mating strategies: Buss & Schmitt, 1993; Schmitt, Shackelford, & Buss, 2001). Empirically, there is mixed evidence for the clustering together of early reproductive maturation and higher number of sexual partners (K. G. Anderson, 2017; Copeland et al., 2010; Ostovich & Sabini, 2005). ‘Short-term mating’ also does not necessarily associate with the ‘fast’ life history trait of higher numbers of offspring: men can achieve high fertility through polygyny or serial monogamy, neither of which necessarily involve short-term mating, at least if short-term mating is defined as a relationship no longer than required to produce a pregnancy (Forsberg & Tullberg, 1995; Heath & Hadley, 1998; Kaar, Jokela, Merila, Helle, & Kojola, 1998). Women may be able to produce many children in quick succession more effectively by remaining with the same partner, because of the time costs involved in switching partners (G. R. Brown, Laland, & Mulder, 2009; but see Mulder, 2009).

If greater interest in sex is considered part of a 'fast life history strategy' then fast life history strategists should better form long-term partnerships, since data often shows that those in long-term relationships have more sex (Twenge, Sherman, & Wells, 2017). Further, sexual behaviour also tends to be variable over time and space, likely at least partly due to shifting cultural norms; the UK National Survey of Sexual Attitudes and Lifestyles has shown quite rapid shifts in sexual behaviour just in the last few decades (Mercer et al., 2013; see also: Scott, Wellings, & Lindberg, 2020). It might therefore be worth reconsidering some of the assumptions regarding short-term and long-term mating which are used in the psychological life history literature.

Cooperative breeding: none of the approaches to human life history fully take into consideration our cooperative breeding strategy (Hrdy, 2006), but all could usefully pay more attention to this aspect of our life history. Our cooperative reproduction will have implications for the allocation of energy between different life history traits, and for our developmental psychology. For example, the use of 'attachment' in infancy as a proximate mechanism through which later life behaviour is calibrated to the environment has been criticised as potentially problematic in anthropology, for focusing too much on the mother as caregiver (LeVine, 2014; Morelli et al., 2018; Otto & Keller, 2014). This excludes the influence of the other individuals who typically care for children in most societies (Crittenden & Marlowe, 2008; Kramer, 2005; Meehan, 2005; Page et al., n.d.). Models of the early development of life history which focus on the cooperative childrearing that most children experience may be more productive in understanding the mechanisms through which early stress affects later life traits, especially in populations which place less emphasis on the nuclear family than WEIRD societies (Amir & McAuliffe, 2020; Clancy & Davis, 2019; Geronimus, 1992; Morelli, Henry, & Spielvogel, 2019; Sear, 2016).

Conclusion

The recent burgeoning of interest in human life history strategy has not been without criticism. All approaches suffer from having increasingly drifted away from life history research in evolutionary biology, and from a lack of theoretical formalisation, meaning that verbal arguments are often made about what 'life history theory predicts' which are not firmly grounded in formal theory. However, incorporating insights from life history research in evolutionary biology, such as the trade-off between reproduction and survival, into the health and social sciences has considerable potential to improve our understanding of human health and behaviour. It is therefore important to strengthen this research programme.

This life history literature could move forward productively by remaining grounded in the life history trade-offs which underlie 'life history strategies', and by ensuring that the 'fast-slow continuum' is used only as a useful heuristic. This would allow for a flexible approach to 'life history strategies', which would encompass domain- and context-specific strategies, rather than assuming a single continuum. As well as greater use of formal theory, this research area also needs more empirical data on linkages between life history and behavioural traits, the environment, and mechanisms which mediate such linkages; and to ensure that the relationship between theory and data is iterative. This includes, importantly, collecting data from a broad range of populations. Without research from diverse human populations, our understanding of whether humans have an adaptive capacity for varying their life history strategy according to environmental conditions will remain limited. It is this relationship between the environment and life history and behavioural traits which is of particular importance if this research is to be used to improve human health and wellbeing.

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References

Alami, S., Stieglitz, J., Kaplan, H., & Gurven, M. (2018). Low perceived control over health is associated with lower treatment uptake in a high mortality population of Bolivian forager-farmers. *Social Science & Medicine*, *200*, 156–165. https://doi.org/10.1016/J.SOCSCIMED.2018.01.017

Allal, N., Sear, R., Prentice, A. M., & Mace, R. (2004). An evolutionary model of stature, age at first birth and reproductive success in Gambian women. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *271*(1538), 465–470. https://doi.org/10.1098/rspb.2003.2623

Allen, G., Eriksson, A. W., Fellman, J., Poinsi, P., & Vandenberg, S. G. (1992). Twinning and the r/K reproductive strategy: a critique of Rushton's theory. *Acta Genet.Med.Gemellol.*, *41*, 73–83.

Alvergne, A., Jenkinson, C., & Faurie, C. (2016). *Evolutionary Thinking in Medicine From Research to Policy and Practice*. Springer.

Amir, D., & McAuliffe, K. (2020). Cross-cultural, developmental psychology: integrating approaches and key insights. *Evolution and Human Behavior*. https://doi.org/10.1016/j.evolhumbehav.2020.06.006

Anderhub, V., Güth, W., Gneezy, U., & Sonsino, D. (2001). On the interaction of risk and time preferences: An experimental study. *German Economic Review*, *2*(3), 239–253. https://doi.org/10.1111/1468-0475.00036

Anderson, J. L. (1991). Rushton's racial comparisons: An ecological critique of theory and method. *Canadian Psychology/Psychologie Canadienne*, *32*(1), 51–62. https://doi.org/10.1037/h0078956

Anderson, K. G. (2010). Life expectancy and the timing of life history events in developing countries. *Human Nature*, *21*(2), 103–123. https://doi.org/10.1007/s12110-010-9087-z

Anderson, K. G. (2017). Adverse Childhood Environment: Relationship With Sexual Risk Behaviors and Marital Status in a Large American Sample. *Evolutionary Psychology : An International Journal of Evolutionary Approaches to Psychology and Behavior*, *15*(2), 1474704917710115. https://doi.org/10.1177/1474704917710115

André, J. B., & Rousset, F. (2020). Does extrinsic mortality accelerate the pace of life? A bare-bones approach. *Evolution and Human Behavior*. https://doi.org/10.1016/j.evolhumbehav.2020.03.002

Andreoni, J., & Sprenger, C. (2012). Risk preferences are not time preferences. *American Economic Review*, *102*(7), 3357–3376. https://doi.org/10.1257/aer.102.7.3357

Barbaro, N., Boutwell, B. B., Barnes, J. C., & Shackelford, T. K. (2017). Genetic confounding of the relationship between father absence and age at menarche. *Evolution and Human Behavior*, *38*(3), 357–365. https://doi.org/10.1016/J.EVOLHUMBEHAV.2016.11.007

Barrett, H. C. (2020). Deciding what to observe: Thoughts for a post-WEIRD generation. *Evolution & Human Behavior*.

Belsky, J. (2005). Differential susceptibility to rearing influence: an evolutionary hypothesis and some evidence. In B. Ellis & D. Bjorklund (Eds.), *Origins of the Social Mind: Evolutionary Psychology* *and Child Development* (pp. 139–163). New York: Guilford.

Belsky, J. (2012). The Development of Human Reproductive Strategies. *Current Directions in Psychological Science*, *21*(5), 310–316. https://doi.org/10.1177/0963721412453588

Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood Experience, Interpersonal Development, and Reproductive Strategy: An Evolutionary Theory of Socialization. *Child Development*, *62*(4), 647–670. https://doi.org/10.1111/j.1467-8624.1991.tb01558.x

Benn Torres, J. (2019). Anthropological perspectives on genomic data, genetic ancestry, and race. *American Journal of Physical Anthropology*, ajpa.23979. https://doi.org/10.1002/ajpa.23979

Bergmüller, R. (2010). Animal personality and behavioural syndromes. In *Animal Behaviour: Evolution and Mechanisms* (pp. 587–621). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-02624-9_19

Bernardi, L., Huinink, J., & Settersten, R. A. (2019). The life course cube: A tool for studying lives. *Advances in Life Course Research*, *41*, 100258. https://doi.org/10.1016/j.alcr.2018.11.004

Bielby, J., Mace, G. M., Bininda-Emonds, O. R. P., Cardillo, M., Gittleman, J. L., Jones, K. E., … Purvis, A. (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation. *The American Naturalist*, *169*(6), 748–757. https://doi.org/10.1086/516847

Black, C. J., Figueredo, A. J., & Jacobs, W. J. (2017). Substance, History, and Politics. *Evolutionary Psychology*, *15*(1), 147470491667040. https://doi.org/10.1177/1474704916670402

Blolund, E. (2020). The challenge of measuring trade-offs in human life history research. *Evolution & Human Behavior*.

Bogin, B., Silva, M. I. V., & Rios, L. (2007). Life history trade-offs in human growth: Adaptation or pathology? *American Journal of Human Biology*, *19*(5), 631–642. https://doi.org/10.1002/ajhb.20666

Borgerhoff Mulder, M. (1998). Brothers and sisters: how sibling interactions affect optimal parental allocations. *Human Nature*, *9*(2), 119–161.

Brown, G. R., Laland, K. N., & Mulder, M. B. (2009). Bateman's principles and human sex roles. *Trends in Ecology & Evolution*, *24*(6), 297–304. Retrieved from http://www.sciencedirect.com/science/article/B6VJ1-4W6X063-1/2/41ff2e5124e052498c4c89e67f178838

Brown, L. J., & Sear, R. (n.d.). Do parenting, reproductive and health traits cluster together in distinct trajectories? Evidence from two UK cohort studies. https://doi.org/10.31219/OSF.IO/R8JVW

Brown, L. J., & Sear, R. (2017). Local environmental quality positively predicts breastfeeding in the UK's Millennium Cohort Study. *Evolution, Medicine, and Public Health*, *2017*(1), 120–135. https://doi.org/10.1093/emph/eox011

Brumbach, B. H., Figueredo, A. J., & Ellis, B. J. (2009). Effects of harsh and unpredictable environments in adolescence on development of life history strategies: A Longitudinal Test of an Evolutionary Model. *Human Nature*, *20*(1), 25–51. https://doi.org/10.1007/s12110-009-9059-3

Buss, D. M., & Schmitt, D. P. (1993). Sexual Strategies Theory: An Evolutionary Perspective on Human Mating. *Psychological Review*, *100*(2), 204–232. https://doi.org/10.1037/0033-295X.100.2.204

Cain, D. P., & Vanderwolf, C. H. (1990). A critique of Rushton on race, brain size and intelligence. *Personality and Individual Differences*, *11*(8), 777–784. https://doi.org/10.1016/0191-

8869(90)90185-T

Cernovsky, Z. Z. (1990). Race and brain weight: a note on J.P. Rushton's conclusions. *Psychological Reports*, *66*(1), 337–338. https://doi.org/10.2466/pr0.1990.66.1.337

Charnov, E. L. (1993). *Life History Invariants*. Oxford: Oxford University Press.

Chisholm, J. S. (1993). Death, hope, and sex: life-history theory and the development of reproductive strategies. *Current Anthropology*, *34*(1), 1–24.

Chisholm, J. S. (1999). Attachment and time preference: relations between early stress and sexual behavior in a sample of American university women. *Human Nature*, *10*(1), 51–83.

Chisholm, J. S., Quinlivan, J. A., Petersen, R. W., & Coall, D. A. (2005). Early stress predicts age at menarche and first birth, adult attachment, and expected lifespan. *Human Nature*, *16*(3), 233–265.

Clancy, K. B. H., & Davis, J. L. (2019). Soylent Is People, and WEIRD Is White: Biological Anthropology, Whiteness, and the Limits of the WEIRD. *Annual Review of Anthropology*, *48*(1), 169–186. https://doi.org/10.1146/annurev-anthro-102218-011133

Clutterbuck, S., Adams, J., & Nettle, D. (2015). Frequent residential relocations cumulatively accelerate menarche timing in a sample of English adolescent girls. *Journal of Biosocial Science*, *47*(02), 188–202. https://doi.org/10.1017/S0021932014000157

Coall, D. A., & Chisholm, J. S. (2003). Evolutionary perspectives on pregnancy: maternal age at menarche and infant birth weight. *Social Science & Medicine*, *57*(10), 1771–1781.

Coall, D. A., Tickner, M., McAllister, L., & Sheppard, P. (2016). Developmental Influences on Fertility Decisions by Women: An Evolutionary Perspective. *Philosophical Transactions of the Royal Society B, Biological Sciences*.

Copeland, W., Shanahan, L., Miller, S., Costello, E. J., Angold, A., & Maughan, B. (2010). Outcomes of early pubertal timing in young women: A prospective population-based study. *American Journal of Psychiatry*, *167*(10), 1218–1225. https://doi.org/10.1176/appi.ajp.2010.09081190

Copping, L. T., Campbell, A., & Muncer, S. (2014). Psychometrics and Life History Strategy: The Structure and Validity of the High K Strategy Scale. *Evolutionary Psychology*, *12*(1). https://doi.org/10.1177/147470491401200115

Copping, L. T., Campbell, A., Muncer, S., & Richardson, G. B. (2017). The Psychometric Evaluation of Human Life Histories. *Evolutionary Psychology*, *15*(1), 147470491666372. https://doi.org/10.1177/1474704916663727

Copping, L. T., & Richardson, G. B. (2020). Studying Sex Differences in Psychosocial Life History Indicators. *Evolutionary Psychological Science*, *6*(1), 47–59. https://doi.org/10.1007/s40806-019-00211-2

Crittenden, A. N., & Marlowe, F. W. (2008). Allomaternal care among the Hadza of Tanzania. *Human Nature-an Interdisciplinary Biosocial Perspective*, *19*(3), 249–262. https://doi.org/10.1007/s12110-008-9043-3

Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018, March 1). Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. *Behavioral Ecology and Sociobiology*. Springer Verlag. https://doi.org/10.1007/s00265-018-2473-y

Del Giudice, M. (2009). Sex, attachment, and the development of reproductive strategies. *Behavioral* *and Brain Sciences*, *32*(1), 1–21. Retrieved from http://journals.cambridge.org/action/displayFulltext?type=6&fid=3920656&jid=&volumeId=&issueId=01&aid=3920652&bodyId=&membershipNumber=&societyETOCSession=&fulltextType=RA&fileId=S0140525X09000016#

Del Giudice, M. (2020, May 20). Rethinking the fast-slow continuum of individual differences. *Evolution and Human Behavior*. Elsevier Inc. https://doi.org/10.1016/j.evolhumbehav.2020.05.004

Del Giudice, M., & Belsky, J. (2011). The development of life history strategies: toward a multi-stage theory. In D. M. Buss & P. H. Hawley (Eds.), *The Evolution of Personality and Individual Differences* (pp. 154–176). Oxford: Oxford University Press.

Del Giudice, M., Ellis, B. J., & Shirtcliff, E. A. (2011, June 1). The Adaptive Calibration Model of stress responsivity. *Neuroscience and Biobehavioral Reviews*. Pergamon. https://doi.org/10.1016/j.neubiorev.2010.11.007

DelPriore, D. J., Proffitt Leyva, R., Ellis, B. J., & Hill, S. E. (2018). The effects of paternal disengagement on women's perceptions of male mating intent. *Journal of Personality and Social Psychology*, *114*(2), 286–302. https://doi.org/10.1037/pspi0000113

Doblhammer, G., & Oeppen, J. (2003). Reproduction and longevity among the British peerage: the effect of frailty and health selection. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *270*(1524), 1541–1547.

Dobzhansky, T. (1950). Evolution in the Tropics. *American Scientist*, *38*, 209–221. Retrieved from http://people.wku.edu/charles.smith/biogeog/DOBZ1950.htm

Draper, P., & Harpending, H. (1982). Father absence and reproductive strategy: an evolutionary perspective. *Journal of Anthropological Research*, *38*(3), 255–273.

Ellis, B. J. (2004). Timing of Pubertal Maturation in Girls: An Integrated Life History Approach. *Psychological Bulletin*, *130*(6), 920–958.

Ellis, B. J., & Del Giudice, M. (2019). Developmental Adaptation to Stress: An Evolutionary Perspective. *Annual Review of Psychology*, *70*(1). https://doi.org/10.1146/annurev-psych-122216-011732

Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). Fundamental Dimensions of Environmental Risk. *Human Nature*, *20*(2), 204–268. https://doi.org/10.1007/s12110-009-9063-7

Ellison, P. T. (1990). Human ovarian function and reproductive ecology: new hypotheses. *American Anthropologist*, *92*(4), 933–952.

Ellison, P. T. (2003). Energetics and reproductive effort. *American Journal of Human Biology*, *15*(3), 342–351.

Ellison, P. T. (2017). Endocrinology, energetics, and human life history: A synthetic model. *Hormones and Behavior*, *91*, 97–106. https://doi.org/10.1016/j.yhbeh.2016.09.006

Ellison, P. T., Reiches, M. W., Shattuck-Faegre, H., Breakey, A., Konecna, M., Urlacher, S., & Wobber, V. (2012). Puberty as a life history transition. *Annals of Human Biology*, *39*(5), 352–360. https://doi.org/10.3109/03014460.2012.693199

Figueredo, A. J., de Baca, T. C., Black, C. J., García, R. A., Fernandes, H. B. F., Wolf, P. S. A., & Anthony, M. (2015). Methodologically Sound: Evaluating the Psychometric Approach to the Assessment of Human Life History [Reply to]. *Evolutionary Psychology*, *13*(2), 147470491501300.

https://doi.org/10.1177/147470491501300202

Figueredo, A. J., Garcia, R. A., Menke, J. M., Jacobs, W. J., Gladden, P. R., Bianchi, J., … Li, N. P. (2017). The K-SF-42: A New Short Form of the Arizona Life History Battery. *Evolutionary Psychology*, *15*(1), 147470491667627. https://doi.org/10.1177/1474704916676276

Figueredo, A. J., Vasquez, G., Brumbach, B. H., & Schneider, S. M. R. (2007). The K-factor, covitality, and personality: a psychometric test of life history theory. *Human Nature-an Interdisciplinary Biosocial Perspective*, *18*(1), 47–73.

Figueredo, A. J., Vásquez, G., Brumbach, B. H., & Schneider, S. M. R. (2004). The heritability of life history strategy: the K-factor, covitality, and personality. *Social Biology*, *51*(3–4), 121–143. https://doi.org/10.1080/19485565.2004.9989090

Figueredo, A. J., Vásquez, G., Brumbach, B. H., Schneider, S. M. R., Sefcek, J. A., Tal, I. R., … Jacobs, W. J. (2006). Consilience and Life History Theory: From genes to brain to reproductive strategy. *Developmental Review*, *26*(2), 243–275. https://doi.org/10.1016/j.dr.2006.02.002

Figueredo, A. J., Vásquez, G., Brumbach, B. H., Sefcek, J. A., Kirsner, B. R., & Jacobs, W. J. (2005). The K-factor: Individual differences in life history strategy. *Personality and Individual Differences*, *39*(8), 1349–1360. https://doi.org/10.1016/j.paid.2005.06.009

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.

Forsberg, A. J. L., & Tullberg, B. S. (1995). The relationship between cumulative number of cohabiting partners and number of children for men and women in modern Sweden. *Ethology and Sociobiology*, *16*(3), 221–232.

Frankenhuis, W. E., & Nettle, D. (2020). The Strengths of People in Poverty. *Current Directions in Psychological Science*, *29*(1), 16–21. https://doi.org/10.1177/0963721419881154

Frankenhuis, W. E., Panchanathan, K., & Nettle, D. (2016). Cognition in harsh and unpredictable environments. *Current Opinion in Psychology*, *7*, 76–80. https://doi.org/10.1016/j.copsyc.2015.08.011

Frankenhuis, W. E., & Tiokhin, L. (2018). Bridging Evolutionary Biology and Developmental Psychology: Toward An Enduring Theoretical Infrastructure. *Child Development*, *89*(6), 2303–2306. https://doi.org/10.1111/cdev.13021

Geronimus, A. T. (1992). The weathering hypothesis and the health of African-American women and infants: evidence and speculations. *Ethnicity & Disease*, *2*(3), 207–221. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1467758

Geronimus, A. T., James, S. A., Destin, M., Graham, L. F., Hatzenbuehler, M. L., Murphy, M. C., … Thompson, J. P. (2016). Jedi public health: Co-creating an identity-safe culture to promote health equity. *SSM - Population Health*, *2*, 105–116. https://doi.org/10.1016/J.SSMPH.2016.02.008

Gettler, L. T., McDade, T. W., Bragg, J. M., Feranil, A. B., & Kuzawa, C. W. (2015). Developmental energetics, sibling death, and parental instability as predictors of maturational tempo and life history scheduling in males from Cebu, Philippines. *American Journal of Physical Anthropology*, *158*(2), 175–184. https://doi.org/10.1002/ajpa.22783

Gibson, M. A., & Lawson, D. W. (Eds.). (2014). *Applied Evolutionary Anthropology*. New York, NY: Springer New York. https://doi.org/10.1007/978-1-4939-0280-4

Gibson, M. A., & Mace, R. (2006). An energy-saving development initiative increases birth rate and childhood malnutrition in rural Ethiopia. *PLos Medicine*, *3*(4), e87.

Gruijters, S. L. K., & Fleuren, B. P. I. (2018). Measuring the Unmeasurable. *Human Nature*, *29*(1), 33–44. https://doi.org/10.1007/s12110-017-9307-x

Gurven, M., Costa, M., Ben Trumble, Stieglitz, J., Beheim, B., Eid Rodriguez, D., … Kaplan, H. (2016). Health costs of reproduction are minimal despite high fertility, mortality and subsistence lifestyle. *Scientific Reports*, *6*(1), 1–10. https://doi.org/10.1038/srep30056

Heath, K. M., & Hadley, C. (1998). Dichotomous male reproductive strategies in a polygynous human society. Mating versus parental effort. *Current Anthropology*, *39*(3), 369–374.

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, *33*(2–3), 61–83. https://doi.org/doi:10.1017/S0140525X0999152X

Hentges, R. F., Shaw, D. S., & Wang, M. Te. (2018). Early childhood parenting and child impulsivity as precursors to aggression, substance use, and risky sexual behavior in adolescence and early adulthood. *Development and Psychopathology*, *30*(4), 1305–1319. https://doi.org/10.1017/S0954579417001596

Hill, K. (1993). Life history theory and evolutionary anthropology. *Evolutionary Anthropology*, *2*(3), 78–88.

Hill, K., & Hurtado, A. M. (1996). *Ache Life History: The Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter.

Houghton, L. C., Cooper, G. D., Booth, M., Chowdhury, O. A., Troisi, R., Ziegler, R. G., … Bentley, G. R. (2014). Childhood Environment Influences Adrenarcheal Timing among First-Generation Bangladeshi Migrant Girls to the UK. *PLoS ONE*, *9*(10), e109200. https://doi.org/10.1371/journal.pone.0109200

Hrdy, S. B. (2006). Evolutionary context of human development: the cooperative breeding model. In C. S. Carter, L. Ahnert, K. E. Grossman, S. B. Hrdy, & M. E. Lamb (Eds.), *Attachment and Bonding: A New Synthesis*. Harvard: MIT Press.

Hrdy, S. B. (2009). *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Cambridge, Massachusetts: Belknap Press.

Jasienska, G. (2003). Energy metabolism and the evolution of reproductive suppression in the human female. *Acta Biotheoretica*, *51*(1), 1–18.

Jasienska, G. (2009). Reproduction and lifespan: trade-offs, overall energy budgets, intergenerational costs and costs neglected by research. *American Journal of Human Biology*.

Jasienska, G. (2011). Why energy expenditure causes reproductive suppression in women: an evolutionary and bioenergetic perspective. In P. T. Ellison (Ed.), *Reproductive Ecology and Human Evolution* (pp. 59–84). Aldine de Gruyter.

Jasienska, G., & Ellison, P. T. (1998). Physical work causes suppression of ovarian function in women. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *265*(1408), 1847–1851.

Jones, O. R., Ezard, T. H. G., Dooley, C., Healy, K., Hodgson, D. J., Mueller, M., … Salguero-Gomez, R. (n.d.). *My family and other animals: Human demography under a comparative cross-species lens*. Retrieved from https://osf.io/ehp92/

Jones, O. R., Scheuerlein, A., Salguero-Gomez, R., Camarda, C. G., Schaible, R., Casper, B. B., … Vaupel, J. W. (2014). Diversity of ageing across the tree of life. *Nature*, *505*(7482), 169–173. Retrieved from http://dx.doi.org/10.1038/nature12789

Kaar, P., Jokela, J., Merila, J., Helle, T., & Kojola, I. (1998). Sexual conflict and remarriage in preindustrial human populations: Causes and fitness consequences. *Evolution and Human Behavior*, *19*(3), 139–151.

Kaplan, H. (1996). A theory of fertility and parental investment in traditional and modern human societies. *Yearbook of Physical Anthropology*, *39*, 91–135.

Kaplan, H., & Lancaster, J. (2000). The evolutionary economics and psychology of the demographic transition to low fertility. In L. Cronk, N. Chagnon, & W. Irons (Eds.), *Adaptation and Human Behaviour: an Anthropological Perspective* (pp. 283–321). New York: Aldine de Gruyter.

Kaplan, H., Lancaster, J., & Robson, A. (2003). Embodied capital and the evolutionary economics of the human lifespan. *Population and Development Review*, *29*(Supplement: Lifespan: Evolutionary, Ecology and Demographic Perspectives. Eds J.R. Carey & S. Tuljapakur), 152–182.

Kokko, H., & Jennions, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, *21*(4), 919–948. https://doi.org/10.1111/j.1420-9101.2008.01540.x

Kramer, K. L. (2005). Children's help and the pace of reproduction: cooperative breeding in humans. *Evolutionary Anthropology*, *14*(6), 224–237.

Kramer, K. L., & Ellison, P. T. (2010). Pooled energy budgets: Resituating human energy -allocation trade-offs. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*(4), 136–147. https://doi.org/10.1002/evan.20265

Kramer, K. L., Greaves, R. D., & Ellison, P. T. (2009). Early reproductive maturity among Pumé foragers: implications of a pooled energy budget to fast life histories. *American Journal of Human Biology*.

Krebs, J. R., & Davies, N. B. (1991). *Behavioural Ecology: an Evolutionary Approach* (3rd editio). Oxford: Blackwell Science.

Kruger, D. J., & Fisher, M. L. (2008). Women's Life History Attributes are Associated with Preferences in Mating Relationships. *Evolutionary Psychology*, *6*(2), 147470490800600. https://doi.org/10.1177/147470490800600206

Kuzawa, C. W., & Bragg, J. M. (2012, December 17). Plasticity in human life history strategy: Implications for contemporary human variation and the evolution of genus Homo. *Current Anthropology*. University of Chicago PressChicago, IL. https://doi.org/10.1086/667410

Kuziez, D., Harkey, J., Burack, S., Borja, J., & Quinn, E. A. (2020). Maternal birth weight is associated with milk epidermal growth factor in Filipino women. *American Journal of Human Biology*. https://doi.org/10.1002/ajhb.23403

Kyweluk, M. A., Georgiev, A. V., Borja, J. B., Gettler, L. T., & Kuzawa, C. W. (2018). Menarcheal timing is accelerated by favorable nutrition but unrelated to developmental cues of mortality or familial instability in Cebu, Philippines. *Evolution and Human Behavior*, *39*(1), 76–81. https://doi.org/10.1016/J.EVOLHUMBEHAV.2017.10.002

Lack, D. (1954). The evolution of reproductive rates. In J. S. Huxley, A. C. Hardy, & E. B. Ford (Eds.), *Evolution as a Process* (pp. 143–156). London: Allen and Unwin.

Lancaster, J. B., & Kaplan, H. (2009). The endocrinology of the human adaptive complex. In P. G. Gray & P. T. Ellison (Eds.), *Endocrinology of Social Relationships*. Cambridge, MA: Harvard University Press.

Law, R. (1979). Optimal Life Histories Under Age-Specific Predation. *The American Naturalist*, *114*(3), 399–417. https://doi.org/10.1086/283488

Lawn, R. B., Sallis, H. M., Wootton, R. E., Taylor, A. E., Demange, P., Fraser, A., … Munafò, M. R. (2020). The effects of age at menarche and first sexual intercourse on reproductive and behavioural outcomes: A Mendelian randomization study. *PLOS ONE*, *15*(6), e0234488. https://doi.org/10.1371/journal.pone.0234488

Lawson, D. W., Alvergne, A., & Gibson, M. A. (2012). The life-history trade-off between fertility and child survival. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1748), 4755–4764. https://doi.org/10.1098/rspb.2012.1635

Lawson, D. W., & Borgerhoff Mulder, M. (2016). The offspring quantity-quality trade-off and human fertility variation. *Philosophical Transactions of the Royal Society B, Biological Sciences*.

LeVine, R. A. (2014). Attachment theory as cultural ideology. In H. Otto & H. Keller (Eds.), *Different Faces of Attachment: Cultural Variations on a Universal Human Need* (pp. 50–65). Cambridge, UK: Cambridge University Press.

Longman, D. P., Wells, J. C. K., & Stock, J. T. (2020). Human athletic paleobiology; using sport as a model to investigate human evolutionary adaptation. *American Journal of Physical Anthropology*, *171*(S70), 42–59. https://doi.org/10.1002/ajpa.23992

Low, B. S., Hazel, A., Parker, N., & Welch, K. B. (2008). Influences on women’s reproductive lives: unexpected ecological underpinnings. *Cross-Cultural Research*, *42*(3), 201–219. https://doi.org/10.1177/1069397108317669

Lummaa, V. (2003). Early developmental conditions and reproductive success in humans: Downstream effects of prenatal famine, birthweight, and timing of birth. *American Journal of Human Biology*, *15*(3), 370–379.

Lycett, J. E., Dunbar, R. I. M., & Voland, E. (2000). Longevity and the costs of human reproduction in a historical human population. *Proceedings of the Royal Society of London, Series B*, *267*, 31–35.

Lynn, M. (1989, March 1). Race differences in sexual behavior: A critique of Rushton and Bogaert’s evolutionary hypothesis. *Journal of Research in Personality*. Academic Press. https://doi.org/10.1016/0092-6566(89)90029-9

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press.

Mace, R. (2000). The evolutionary ecology of human life history. *Animal Behaviour*, *59*, 1–10.

Manson, J. H., Chua, K. J., & Lukaszewski, A. W. (2020). The Structure of the Mini-K and K-SF-42: A Psychological Network Approach. *Human Nature*, 1–19. https://doi.org/10.1007/s12110-020-09373-6

Martin, M. A., & Valeggia, C. (2018). Timing of pubertal growth and menarche in indigenous Qom girls of Argentina. *Annals of Human Biology*, 1–9. https://doi.org/10.1080/03014460.2018.1486455

Mathes, E. W. (2018). Life History Theory and Tradeoffs: an Obituary Study. *Evolutionary Psychological Science*, *4*(4), 391–398. https://doi.org/10.1007/s40806-018-0144-x

Mathot, K. J., & Frankenhuis, W. E. Models of pace-of-life syndromes (POLS): a systematic review, 72 Behavioral Ecology and Sociobiology § (2018). https://doi.org/10.1007/s00265-018-2459-9

McAllister, L., Pepper, G., Virgo, S., & Coall, D. A. (2016). The Evolved Psychological Mechanisms of Fertility Motivation: Hunting for Causation in a Sea of Correlation. *Philosophical Transactions of the Royal Society B, Biological Sciences*.

McElreath, R., Luttbeg, B., Fogarty, S. P., Brodin, T., & Sih, A. (2007, November 8). Evolution of animal personalities. *Nature*. Nature Publishing Group. https://doi.org/10.1038/nature06326

Međedović, J. (n.d.). On the incongruence between psychometric and psychosocial-biodemographic measures of life history. Retrieved August 14, 2020, from https://www.researchgate.net/publication/343136517_On_the_incongruence_between_psychometric_and_psychosocial-biodemographic_measures_of_life_history_manuscript_in_press

Meehan, C. L. (2005). The effects of residential locality on parental and alloparental investment among the Aka foragers of the Central African Republic. *Human Nature*, *16*(1), 58–80.

Meehan, C. L., Quinlan, R., & Malcom, C. D. (2013). Cooperative breeding and maternal energy expenditure among Aka foragers. *American Journal of Human Biology : The Official Journal of the Human Biology Council*, *25*(1), 42–57. https://doi.org/10.1002/ajhb.22336

Mell, H., Safra, L., Algan, Y., Baumard, N., & Chevallier, C. (2018). Childhood environmental harshness predicts coordinated health and reproductive strategies: A cross-sectional study of a nationally representative sample from France. *Evolution and Human Behavior*, *39*(1), 1–8. https://doi.org/10.1016/J.EVOLHUMBEHAV.2017.08.006

Mercer, C. H., Tanton, C., Prah, P., Erens, B., Sonnenberg, P., Clifton, S., … Johnson, A. M. (2013). Changes in sexual attitudes and lifestyles in Britain through the life course and over time: Findings from the National Surveys of Sexual Attitudes and Lifestyles (Natsal). *The Lancet*, *382*(9907), 1781–1794. https://doi.org/10.1016/S0140-6736(13)62035-8

Mills, M. C., Barban, N., & Tropf, F. C. (2018). The sociogenomics of polygenic scores of reproductive behavior and their relationship to other fertility traits. *RSF*, *4*(4), 122–136. https://doi.org/10.7758/rsf.2018.4.4.07

Morelli, G., Henry, P. I., & Spielvogel, B. (2019, June 1). Learning prosociality: insights from young forager and subsistence farmer children's food sharing with mothers and others. *Behavioral Ecology and Sociobiology*. Springer Verlag. https://doi.org/10.1007/s00265-019-2671-2

Morelli, G., Quinn, N., Chaudhary, N., Vicedo, M., Rosabal-Coto, M., Keller, H., … Takada, A. (2018). Ethical Challenges of Parenting Interventions in Low- to Middle-Income Countries. *Journal of Cross-Cultural Psychology*, *49*(1), 5–24. https://doi.org/10.1177/0022022117746241

Mulder, M. B. (2009). Serial monogamy as polygyny or polyandry?: Marriage in the Tanzanian Pimbwe. *Human Nature*, *20*(2), 130–150. https://doi.org/10.1007/s12110-009-9060-x

Nesse, R. M., & Williams, G. C. (1995). *Why We Get Sick: the New Science of Evolutionary Medicine*. Times Books.

Nettle, D. (2010). Dying young and living fast: variation in life history across English neighborhoods. *Behavioral Ecology* , *21*(2), 387–395. Retrieved from http://beheco.oxfordjournals.org/content/21/2/387.abstract

Nettle, D. (2011). Flexibility in reproductive timing in human females: integrating ultimate and proximate explanations. *Philosophical Transactions of the Royal Society B: Biological Sciences* , *366*(1563), 357–365. Retrieved from http://rstb.royalsocietypublishing.org/content/366/1563/357.abstract

Nettle, D. (2015). *Tyneside Neighbourhoods: Deprivation, Social Life and Social Behaviour in One British City*. Open Book Publishers. https://doi.org/10.11647/OBP.0084

Nettle, D. (2019). Social inequality: The embedding of adversity across the life course. *Scandinavian Journal of Public Health*, *47*(6), 672–677. https://doi.org/10.1177/1403494819857035

Nettle, D., Coall, D. A., & Dickins, T. E. (2010a). Birthweight and paternal involvement affect the likelihood of teenage motherhood: Evidence from the British National Child Development Study. *American Journal of Human Biology*, *22*(2), 172–179.

Nettle, D., Coall, D. A., & Dickins, T. E. (2010b). Early-life conditions and age at first pregnancy in British women. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1712), 1721–1727. https://doi.org/10.1098/rspb.2010.1726

Nettle, D., & Frankenhuis, W. E. (2019). The evolution of life history theory: Bibliometric analysis of an interdisciplinary research area. *Proceedings of the Royal Society B, Series B - Biological Sciences*, *286*(1899), 20190040. https://doi.org/10.1101/510826

Nettle, D., & Frankenhuis, W. E. (2020). Life-history theory in psychology and evolutionary biology: one research programme or two? *Philosophical Transactions of the Royal Society B*, *375*, 20190. https://doi.org/10.1098/RSTB.2019.0490

Nettle, D., Gibson, M. A., Lawson, D. W., & Sear, R. (2013). Human behavioral ecology: current research and future prospects. *Behavioral Ecology*, *24*(5), 1031–1040. https://doi.org/10.1093/beheco/ars222

Nolin, D. A., & Ziker, J. P. (2016). Reproductive Responses to Economic Uncertainty: Fertility Decline in Post-Soviet Ust'-Avam, Siberia. *Human Nature*, *27*(4), 351–371. https://doi.org/10.1007/s12110-016-9267-6

Núñez-de la Mora, A., Chatterton, R. T., Choudhury, O. A., Napolitano, D. A., & Bentley, G. R. (2007). Childhood conditions influence adult progesterone levels. *PLoS Medicine*, *4*(5), e167. https://doi.org/10.1371/journal.pmed.0040167

Ostovich, J. M., & Sabini, J. (2005). Timing of puberty and sexuality in men and women. *Archives of Sexual Behavior*, *34*(2), 197–206. https://doi.org/10.1007/s10508-005-1797-7

Otto, H., & Keller, H. (2014). *Different Faces of Attachment: Cultural Variations on a Universal Human Need*. Cambridge University Press. Retrieved from https://books.google.com/books?hl=en&lr=&id=xqYdBAAAQBAJ&pgis=1

Page, A. E., Emmott, E. H., Dyble, M., Smith, D., Chaudhary, N., Viguier, S., & Migliano, A. B. (n.d.). Children are important too: juvenile playgroups and maternal childcare in a foraging population, the Agta. *OSF Preprint*. https://doi.org/10.31219/osf.io/8xuj2

Parker, G. A., & Maynard Smith, J. (1990). Optimality theory in evolutionary biology. *Nature*, *348*, 27–33.

Penn, D. J., & Smith, K. R. (2007). Differential fitness costs of reproduction between the sexes. *PNAS*, *104*(2), 553–558. https://doi.org/10.1073/pnas.0609301103

Pennington, R., & Harpending, H. (1993). *The Structure of an African Pastoralist Community: Demography, History and Ecology of the Ngamiland Herero.* Oxford: Clarendon Press.

Pepper, G. V., & Nettle, D. (2014a). Out of control mortality matters: the effect of perceived uncontrollable mortality risk on a health-related decision. *PeerJ*, *2*, e459. https://doi.org/10.7717/peerj.459

Pepper, G. V., & Nettle, D. (2014b). Perceived Extrinsic Mortality Risk and Reported Effort in Looking after Health. *Human Nature*, *25*(3), 378–392. https://doi.org/10.1007/s12110-014-9204-5

Pepper, G. V., & Nettle, D. (2014c). Socioeconomic Disparities in Health Behaviour: An Evolutionary Perspective. In *Applied Evolutionary Anthropology* (pp. 225–243). New York, NY: Springer New York. https://doi.org/10.1007/978-1-4939-0280-4_10

Pepper, G. V., & Nettle, D. (2017). The behavioural constellation of deprivation: Causes and consequences. *Behavioral and Brain Sciences*, *40*, e314. https://doi.org/10.1017/S0140525X1600234X

Pianka, E. R. (1970). On r- and K-Selection. *The American Naturalist*, *104*(940), 592–597. https://doi.org/10.1086/282697

Placek, C. D., & Quinlan, R. J. (2012). Adolescent fertility and risky environments: a population-level perspective across the lifespan. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4003–4008. https://doi.org/10.1098/rspb.2012.1022

Promislow, D. E. L., & Harvey, P. H. (1990). Living fast and dying young: a comparative analysis of life history variation among mammals. *Journal of Zoology*, *220*, 417–437.

Quinlan, R. J., & Quinlan, M. B. (2007). Parenting and cultures of risk: a comparative analysis of infidelity, aggression, and witchcraft. *American Anthropologist*, *109*(1), 164–179. https://doi.org/doi:10.1525/aa.2007.109.1.164

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010, December 27). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*. Royal Society. https://doi.org/10.1098/rstb.2010.0208

Reiches, M. W., Ellison, P. T., Lipson, S., Sharrock, K., Gardiner, E., & Duncan, L. G. (2009). Pooled energy budget and human evolution. *American Journal of Human Biology*.

Richardson, G. B., Dariotis, J. K., & Lai, M. H. C. (2017). From Environment to Mating Competition and Super-K in a Predominantly Urban Sample of Young Adults. *Evolutionary Psychology*, *15*(1), 147470491667016. https://doi.org/10.1177/1474704916670165

Richardson, G. B., Placek, C., Srinivas, V., Jayakrishna, P., Quinlan, R., & Madhivanan, P. (2020). Environmental stress and human life history strategy development in rural and peri-urban South India. *Evolution and Human Behavior*, *41*(3), 244–252. https://doi.org/10.1016/j.evolhumbehav.2020.03.003

Richardson, G. B., Sanning, B. K., Lai, M. H. C., Copping, L. T., Hardesty, P. H., & Kruger, D. J. (2017). On the Psychometric Study of Human Life History Strategies. *Evolutionary Psychology*, *15*(1), 147470491666684. https://doi.org/10.1177/1474704916666840

Robson, A., & Kaplan, H. (2005). Why we grow large and then grow old: economics, biology and mortality.

Roff, D. A. (1992). *The Evolution of Life Histories*. New York: Chapman and Hall.

Roff, D. A. (2002). *Life History Evolution*. Sunderland, Massachusetts: Sinauer Associates.

Royauté, R., Berdal, M. A., Garrison, C. R., & Dochtermann, N. A. (2018). Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology*, *72*(3). https://doi.org/10.1007/s00265-018-2472-z

Rushton, J. P. (1985). Differential K theory: The sociobiology of individual and group differences. *Personality and Individual Differences*, *6*(4), 441–452. https://doi.org/10.1016/0191-8869(85)90137-0

Rushton, J. P. (1996). *Race, Evolution and Behavior*. Transaction Publishers.

Rutherford, J. N., Victoria, A. deMartelly, Ragsdale, H. B., Avila, J. L., Lee, N. R., & Kuzawa, C. W. (2019). Global population variation in placental size and structure: Evidence from Cebu, Philippines. *Placenta*, *85*, 40–48. https://doi.org/10.1016/j.placenta.2019.08.076

Salmon, C., Figueredo, A. J., & Woodburn, L. (2009). Life History Strategy and Disordered Eating Behavior. *Evolutionary Psychology*, *7*(4), 147470490900700. https://doi.org/10.1177/147470490900700408

Schmitt, D. P., Shackelford, T. K., & Buss, D. M. (2001). Are men really more “oriented” toward short-term mating than women? A critical review of theory and research. *Psychology, Evolution & Gender*, *3*(3), 211–239. https://doi.org/10.1080/14616660110119331

Scott, R. H., Wellings, K., & Lindberg, L. (2020). Adolescent Sexual Activity, Contraceptive Use, and Pregnancy in Britain and the U.S.: A Multidecade Comparison. In *Journal of Adolescent Health*. Elsevier USA. https://doi.org/10.1016/j.jadohealth.2019.11.310

Sear, R. (2007). The impact of reproduction on Gambian women: does controlling for phenotypic quality reveal costs of reproduction? *American Journal of Physical Anthropology*, *132*(4), 632–641. https://doi.org/10.1002/ajpa.20558

Sear, R. (2010). Height and reproductive success: is bigger always better? In U. Frey, C. Stoermer, & K. Willfuehr (Eds.), *Homo Novus: A Human Without Illusions* (pp. 127–143). Springer.

Sear, R. (2016). Beyond the Nuclear Family: An Evolutionary Perspective on Parenting. *Current Opinion in Psychology*, *7*, 98–103. https://doi.org/10.1016/j.copsyc.2015.08.013

Sear, R. (2020). Strengthening the evolutionary social sciences with more data, less ‘theory-worship.’ *Evolution and Human Behavior*. https://doi.org/10.1016/j.evolhumbehav.2020.07.010

Sear, R., Sheppard, P., & Coall, D. A. (2019). Cross-cultural evidence does not support universal acceleration of puberty in father absent households. *Philosophical Transactions of the Royal Society B, Biological Sciences*.

Sheehy-Skeffington, J. (2020, June 1). The effects of low socioeconomic status on decision-making processes. *Current Opinion in Psychology*. Elsevier B.V. https://doi.org/10.1016/j.copsyc.2019.07.043

Sheehy-Skeffington, J., & Rea, J. (2017). *How poverty affects people’s decision-making processes*. Retrieved from www.jrf.org.uk

Shenk, M. K., Kaplan, H. S., & Hooper, P. L. (2016). Status competition, inequality, and fertility: Implications for the demographic transition. *Philosophical Transactions of the Royal Society B, Biological Sciences*.

Sheppard, P., Garcia, J. R., & Sear, R. (2014). A not-so-grim tale: how childhood family structure influences reproductive and risk-taking outcomes in a historical U.S. Population. *PloS One*, *9*(3), e89539. https://doi.org/10.1371/journal.pone.0089539

Sheppard, P., Garcia, J. R., & Sear, R. (2015). Childhood family disruption and adult height: is there a mediating role of puberty? *Evolution, Medicine, and Public Health*, *2015*(1), 332–342. https://doi.org/10.1093/emph/eov028

Sheppard, P., Pearce, M. S., & Sear, R. (2015). How does childhood socioeconomic hardship affect reproductive strategy? Pathways of development. *American Journal of Human Biology : The Official Journal of the Human Biology Council*, *28*(3). https://doi.org/10.1002/ajhb.22793

Sheppard, P., Schaffnit, S. B., Garcia, J. R., & Sear, R. (2014). Fostering relations: first sex and marital timings for children raised by kin and non-kin carers. *Evolution and Human Behavior*, *35*(3), 161–168. https://doi.org/10.1016/j.evolhumbehav.2013.12.002

Sheppard, P., & Sear, R. (2012). Father absence predicts age at sexual maturity and reproductive timing in British men. *Biology Letters*, *8*(2), 237–240. https://doi.org/10.1098/rsbl.2011.0747

Sheppard, P., & Van Winkle, Z. (2020). Are human life histories really coherent strategies? Using sequence analysis to empirically test a widespread theoretical assumption. *Evolutionary Human Sciences*. Retrieved from https://osf.io/tdk79/

Sng, O., Neuberg, S. L., Varnum, M. E. W., & Kenrick, D. T. (2017). The crowded life is a slow life: Population density and life history strategy. *Journal of Personality and Social Psychology*, *112*(5), 736–754. https://doi.org/10.1037/pspi0000086

Snopkowski, K., & Ziker, J. P. (2019). Sexual initiation among Canadian youth: A model comparison approach of evolutionary hypotheses shows greatest support for extrinsic mortality cues, intergenerational conflict, and early life psychosocial stressors. *Evolution and Human Behavior*, *41*(2), 105–116. https://doi.org/10.1016/j.evolhumbehav.2019.08.003

Stearns, S. C. (1976). Life history tactics. A review of the ideas. *Quarterly Review of Biology*, *51*, 3–47.

Stearns, S. C. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology*, *3*(3), 259. https://doi.org/10.2307/2389364

Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.

Stearns, S. C. (2000). Life history evolution: successes, limitations, and prospects. *Naturwissenschaften*, *87*(11), 476–486.

Stearns, S. C., & Koella, J. C. (1986). The evolution of phenotypic plasticity in life history traits: predictions of reaction norms for age and size at maturity. *Evolution*, *40*(5), 893–913.

Stearns, S. C., & Rodrigues, A. M. M. (2020). On the use of "life history theory" in evolutionary psychology. *Evolution and Human Behavior*. https://doi.org/10.1016/j.evolhumbehav.2020.02.001

Stiver, K. A., & Alonzo, S. H. (2009). Parental and mating effort: is there necessarily a trade-off? *Ethology*, *115*(12), 1101–1126. https://doi.org/10.1111/j.1439-0310.2009.01707.x

Strassmann, B. I., & Gillespie, B. (2002). Life-history theory, fertility and reproductive success in humans. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *269*(1491), 553–562.

Sturge-Apple, M. L., Davies, P. T., Martin, M. J., Cicchetti, D., & Hentges, R. F. (2012). An examination of the impact of harsh parenting contexts on children's adaptation within an evolutionary framework. *Developmental Psychology*, *48*(3), 791–805. https://doi.org/10.1037/a0026908

Tarka, M., Guenther, A., Niemelä, P. T., Nakagawa, S., & Noble, D. W. A. (2018, August 1). Sex differences in life history, behavior, and physiology along a slow-fast continuum: a meta-analysis. *Behavioral Ecology and Sociobiology*. Springer Verlag. https://doi.org/10.1007/s00265-018-2534-2

Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man, 1871-1971* (pp. 136–179). New York: Aldine de Gruyter.

Twenge, J. M., Sherman, R. A., & Wells, B. E. (2017). Declines in Sexual Frequency among American Adults, 1989–2014. *Archives of Sexual Behavior*, *46*(8), 2389–2401. https://doi.org/10.1007/s10508-017-0953-1

Uggla, C., & Mace, R. (2015). Effects of local extrinsic mortality rate, crime and sex ratio on preventable death in Northern Ireland. *Evolution, Medicine, and Public Health*, *2015*(1), eov020. https://doi.org/10.1093/emph/eov020

Uggla, C., & Mace, R. (2016). Local ecology influences reproductive timing in Northern Ireland independently of individual wealth. *Behavioral Ecology*, *27*(1), 158–165. https://doi.org/10.1093/beheco/arv133

Van Arsdale, A. P. (2019). Population Demography, Ancestry, and the Biological Concept of Race. *Annual Review of Anthropology*, *48*(1), 227–241. https://doi.org/10.1146/annurev-anthro-102218-011154

Van Noordwijk, A. J., & De Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life-history tactics. *American Naturalist*, *128*(1), 137–142.

Vineis, P., Delpierre, C., Castagné, R., Fiorito, G., McCrory, C., Kivimaki, M., … Kelly-Irving, M. (2020). Health inequalities: Embodied evidence across biological layers. *Social Science and Medicine*, *246*, 112781. https://doi.org/10.1016/j.socscimed.2019.112781

Virgo, S., & Sear, R. (2016). Area-level mortality and morbidity predict ‘abortion proportion’ in England and Wales. *Evolution and Human Behavior*, *37*(5), 366–375. https://doi.org/10.1016/j.evolhumbehav.2016.03.001

Vitzthum, V. J. (2008). Evolutionary Models of Women’s Reproductive Functioning. *Annual Review of Anthropology*, *37*(1), 53–73. https://doi.org/10.1146/annurev.anthro.37.081407.085112

Vitzthum, V. J., Bentley, G. R., Spielvogel, H., Caceres, E., Thornburg, J., Jones, L., … Chatterton, R. T. (2002). Salivary progesterone levels and rate of ovulation are significantly lower in poorer than in better-off urban-dwelling Bolivian women. *Human Reproduction*, *17*(7), 1906–1913. https://doi.org/10.1093/humrep/17.7.1906

Wagner, J. K., Yu, J.-H., Ifekwunigwe, J. O., Harrell, T. M., Bamshad, M. J., & Royal, C. D. (2017). Anthropologists’ views on race, ancestry, and genetics. *American Journal of Physical Anthropology*, *162*(2), 318–327. https://doi.org/10.1002/ajpa.23120

Walker, R., Gurven, M., Hill, K., Migliano, A., Chagnon, N., De Souza, R., … Yamauchi, T. (2006). Growth rates and life histories in 22 small-scale societies. *American Journal of Human Biology*, *18*, 295–311.

Webster, G. D., Graber, J. A., Gesselman, A. N., Crosier, B. S., & Schember, T. O. (2014). A Life History Theory of Father Absence and Menarche: A Meta-Analysis. *Evolutionary Psychology*, *12*(2), 147470491401200200. https://doi.org/10.1177/147470491401200202

Weigel, R. M., & Blurton Jones, N. G. (1983). Workshop report: Evolutionary life history analysis of human behavior. *Ethology and Sociobiology*, *4*(4), 233–235. https://doi.org/10.1016/0162-3095(83)90015-8

Weizmann, F., Wiener, N. I., Wiesenthal, D. L., & Ziegler, M. (1990). Differential K theory and racial hierarchies. *Canadian Psychology/Psychologie Canadienne*, *31*(1), 1–13. https://doi.org/10.1037/h0078934

Wells, J. C. K. (2010). Maternal capital and the metabolic ghetto: An evolutionary perspective on the transgenerational basis of health inequalities. *American Journal of Human Biology*, *22*(1), 1–17. Retrieved from http://dx.doi.org/10.1002/ajhb.20994

Wells, J. C. K., Cole, T. J., Cortina-Borja, M., Sear, R., Leon, D. A., Marphatia, A. A., … Menezes, A. M. B. (2019). Low Maternal Capital Predicts Life History Trade-Offs in Daughters: Why Adverse Outcomes Cluster in Individuals. *Frontiers in Public Health*, *7*, 206. https://doi.org/10.3389/fpubh.2019.00206

Wells, J. C. K., Nesse, R. M., Sear, R., Johnstone, R. A., & Stearns, S. C. (2017). Evolutionary public health: introducing the concept. *The Lancet*, *390*(10093), 500–509. https://doi.org/10.1016/S0140-6736(17)30572-X

Wells, J. C. K., & Stock, J. T. (2020, May 21). Life History Transitions at the Origins of Agriculture: A Model for Understanding How Niche Construction Impacts Human Growth, Demography and Health. *Frontiers in Endocrinology*. Frontiers Media S.A. https://doi.org/10.3389/fendo.2020.00325

West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

Wilson, M., & Daly, M. (1997). Life expectancy, economic inequality, homicide, and reproductive timing in Chicago neighbourhoods. *British Medical Journal*, *314*(7089), 1271–1274.

Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*(7144), 581–584. https://doi.org/10.1038/nature05835

Woodley of Menie, M. A., Cabeza de Baca, T., Fernandes, H. B. F., Madison, G., Figueredo, A. J., & Peñaherrera Aguirre, M. (2017). Slow and Steady Wins the Race: K Positively Predicts Fertility in the USA and Sweden. *Evolutionary Psychological Science*, *3*(2), 109–117. https://doi.org/10.1007/s40806-016-0077-1

Xu, Y., Norton, S., & Rahman, Q. (2018). Early life conditions, reproductive and sexuality-related life history outcomes among human males: A systematic review and meta-analysis. *Evolution and Human Behavior*, *39*(1), 40–51. https://doi.org/10.1016/J.EVOLHUMBEHAV.2017.08.005

Zhang, L. (2008). Religious affiliation, religiosity, and male and female fertility. *Demographic Research*, *18*, 233–262. https://doi.org/10.4054/DemRes.2008.18.8

Zietsch, B. P., & Sidari, M. J. (2019). A critique of life history approaches to human trait covariation. *Evolution and Human Behavior*. https://doi.org/10.1016/J.EVOLHUMBEHAV.2019.05.007

Ziomkiewicz, A., Sancilio, A., Galbarczyk, A., Klimek, M., Jasienska, G., & Bribiescas, R. G. (2016). Evidence for the cost of reproduction in humans: High lifetime reproductive effort is associated with greater oxidative stress in post-menopausal women. *PLoS ONE*, *11*(1). https://doi.org/10.1371/journal.pone.0145753

Zuckerman, M., & Brody, N. (1988). Oysters, rabbits and people: A critique of “race differences in behaviour” by J.P. Rushton. *Personality and Individual Differences*, *9*(6), 1025–1033. https://doi.org/10.1016/0191-8869(88)90136-5

Table 1: summary of similarities and differences between the main approaches to life histories. Cells reflect predominant interest or practice in each approach, not necessarily exclusive focus

	Between- or within-species analysis?	**Life history trade-offs or strategies?**	**Emphasis on genetic or environmental underpinnings?**	**What traits are incorporated in life history research?**	**Interest in LH traits or strategies as outcome or predictor variables?**	**Populations of study**	**Methods**
LHT-E	Both	Trade-offs (within-species); strategies (between-species)	Both; emphasis on genetic at between-species level, & environmental, within-species	Life history traits (reproduction, growth, health & survival)	Outcome	Non-human animal, and plant species	Formal modelling, experimental data
Pace of life syndrome	Both	Strategies	Both; emphasis on genetic at between-species level, & environmental, within-species	Life history traits, physiological traits, some behaviours (not mating or cooperation)	Outcome	Human, non-human animal, and plant species	Observational data, limited formal modelling
Evolutionary anthropology	Within	Trade-offs	Environmental	Life history traits, some behaviours (parental investment, risk-taking behaviour)	Outcome	Primary data from small-scale subsistence populations & high income countries, secondary data, typically from high income countries	Observational data, limited formal modelling
Evolutionary developmental psychology	Within	Strategies	Environmental	Mostly behaviours, esp those relating to mating and interpersonal relationships, some life history traits, esp puberty	Outcome	Primary and secondary data from high income countries	Observational data, limited formal modelling
Evolutionary personality psychology	Within	Strategies	Genetic	Wide range of behavioural & cognitive traits, not life history traits	Life history strategy often used as predictor variable	Predominantly convenience samples from high income populations	Observational data