



HUMAN EVOLUTIONARY DEMOGRAPHY

EDITED BY
OSKAR BURGER, RONALD LEE AND REBECCA SEAR



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32. Human Evolutionary Demography: Closing Thoughts

Oskar Burger, Ronald Lee, and Rebecca Sear

A complete understanding of demographic patterns and behaviours is not possible without including the role of evolutionary processes. Many challenges in the social sciences, and in demography in particular, can be more readily met if they include the rich collection of perspectives, models, tools, and theories that evolutionary sciences can provide. Perhaps unexpectedly, the benefits of this inclusion can be indirect, as many benefits of an evolutionary perspective may take the form of a new way of approaching an old problem that leads to insights independent of any goal related to isolating the role of natural selection or adaptation. In other cases, the role of adaptation may have been under-appreciated and can lead to a different understanding of the mechanisms involved. To help human evolutionary demography improve going forward, we offer two general recommendations. One is improving the integration of contemporary developments in evolutionary thought about the role of culture and environment, such as dual-inheritance theory, epigenetics, and the role of social learning and cultural transmission. Many of these developments reflect an increasingly sophisticated understanding of cultural processes in the evolutionary social sciences, but also include conceptual improvements in the definition and understanding of core concepts like fitness and heritability. The role of culture may be a productive point of contact between the social sciences and evolutionary social sciences given shared interests in this area. Second is a call to re-invigorate evolutionary demography with some of the classical ideas that come from life history theory and population ecology, such as the use of energy and resource budgets to structure trade-offs, a focus on the role of ecological factors like density and resources, and the use of formal mathematical models.

One over-arching point in these closing thoughts is simply that a complete understanding of demographic patterns and behaviours is not possible without including the role of evolutionary processes. Evolutionary processes have shaped the histories of all human characteristics and contribute to their contemporary variation. The majority of demographic topics could therefore benefit from consideration of how evolutionary processes affect the topic under study. We are not suggesting that evolution should be the focus of every research article or project. For instance, even in the seemingly evolutionary-focused field of cell biology, one might find that the content of many papers is about describing chemical reactions across membranes with extensive focus on description of a chemical reaction and little to no direct reference to adaptation or evolution. Social science can be analogous to this; each individual paper need not focus on adaptation or evolution, as many will focus on pattern description, detailed understanding of processes, or

evaluations of proximate mechanisms. Nevertheless, most social science topics would still be able to connect with processes and explanations grounded in evolutionary approaches. In fact, much of the gain of applying evolutionary explanation to demography has to do with framing demographic variation differently or recognizing the multitude of processes that can contribute to observed patterns. Note, this means we also consider that demographic topics should involve consideration of other disciplinary approaches, such as those from anthropology, public health, or sociology, involving an appreciation of the diversity of demographic processes, and the importance of how context affects them. As such, we are also arguing for even greater multi-disciplinary underpinnings to demography and for greater appreciation of demography across the social and biological sciences.

This volume presents a wonderful collection of chapters that shed light on the potential of evolutionary perspectives to inform research on a wide range of demographic topics. It leaves us with a thorough overview of the tools of the trade, the development of central ideas, and their application to overarching and applied subjects. A classically trained demographer presents the similarities that exist in the study of population, describes the natural complementarity of the approaches, and articulates the importance of top-down approaches in demography (Kreager chapter). We also have a succinct presentation of 10 major topics in evolutionary demography, written from the perspective of someone deeply rooted in evolutionary human sciences who also has an extensive background in demographic methods (Hill chapter). The potential for depth and nuance in a full-spectrum evolutionary approach is illustrated by the Tinbergen chapters (Jones, Vitzthum, Sheppard, Mace); hopefully in a way that alleviates the occasional tendency to (mis-) perceive tension between evolutionary and mainstream demography: evolutionary explanations are typically not alternatives to social science explanations, but complementary to them. We see in some chapters how anthropological and human-ecological frameworks enhance our understanding of how culture and ecology can shape demographic decisions (Shenk, Ugglá, Blurton-Jones, Borgerhoff Mulder).

Several more chapters in this volume show that conventional or mainstream demographic topics like households, family structures, and culture can be fruitfully examined through a lens of evolution without forced invocations of adaptationism (Colleran, Borgerhoff Mulder, Rotkirch, Jennings, Wilfuehr, Lee, Tuljakpurkar). Others demonstrate that a diverse range of applied topics can be better-understood when framed with more deeply rooted evolutionary context, including our understanding of health, cancer, inequality and global development issues (Lawson et al., DeLong, Gurven et al., Pavard and Metcalf, Wells). Taxonomic depth to human variation is given by comparison across the great apes and beyond (Emery Thompson and Jones et al). We also see how evolutionary demography furthers not just our understanding of demographic processes but of evolutionary processes too (van Daalen and Caswell, Lee, Pavard). Fitness is a computationally intensive metric that can often only be measured by proxy, but we nonetheless have a state-of-the-art understanding for its measurement and interpretation (Moorad, Wachter, vanDaalen and Caswell, Orzack and Levitis, Lee).

With the vigour behind the approach well-established by the preceding chapters, we would like to close with a few thoughts about where some of these efforts might head, emphasizing key ideas that we think could use more attention. We also hope to guide interested readers to useful papers and concepts based on admittedly brief treatments of a number of complex ideas. With evolutionary approaches in hand, mainstream demographic topics can be moved

forward without making the research less applied or strictly about adaptation. The emphasis on multiple levels of explanation, multiple processes, and interdisciplinarity are all strengths that can contribute to fundamental demographic questions.

In an article about population growth for *Science*, one of us (RL) noted some shortcomings in common approaches to population forecasts. First, while resource constraints must ultimately limit the underlying positive and negative feedbacks that affect population growth, “population forecasts largely ignore economic and resource constraints.” Second, in the absence of “grand dynamic theories” forecasters tend to use a descriptive framework called the demographic transition (Lee 2011). The strengths of evolutionary demography, as proposed in the chapters of this volume, could be leveraged to help improve both of these shortcomings: (i) the underappreciation of constraints and feedbacks from the environment, and (ii) the reliance on description rather than on dynamical theory. Evolutionary approaches and tools of population and evolutionary ecology can provide dynamic theory and can also provide guidance for how to include ecological factors like population density or differential access to resources, whether the topic is population growth or some other demographic phenomenon.

For “how” human evolutionary demography can provide help like this more effectively, we make two overarching recommendations: embrace the new and appreciate the classic.

Embrace the New

The first is to *embrace the new* (selectively,¹ of course), meaning increased appreciation of recent theoretical and conceptual developments across the evolutionary sciences that are particularly valuable. Specifically, a modern understanding of heritability includes a number of inter-related developments for studying the non-genetic but nonetheless heritable (cross-generational) implications of key processes like cultural learning, social transmission, or epigenetics (Uchiyama, Spicer, and Muthukrishna 2020; Jablonka and Lamb 2014). Genetic evolution interacts with cultural evolution and understanding this interaction needs to be a major priority of evolutionary demography. The investigation and modelling of cultural evolutionary processes is simply called “cultural evolution” but this branch of theory focusing on how genes and culture co-evolve is “dual-inheritance theory” (Henrich and McElreath 2007). Dual-inheritance theory and studies of cultural transmission overlap with what demography knows as ideational approaches to the demographic transition (Cleland and Wilson 1987; Bongaarts and Watkins 1996). Culture and epigenetics both underlie what demography and public health know as household and community effects.

We call appreciating the significance of these processes and theories “new”, in part because they are new relative to the development of natural selection, but there have been some fairly recent syntheses pointing out the importance of these pathways of inheritance for evolutionary theory in general (Laland et al. 2015; Jablonka and Lamb 2014; Uchiyama, Spicer, and Muthukrishna 2020). However, “new” does not imply under-developed. Evolutionary researchers who specialize in culture have a rich architecture of formal models and explicit theory that can help serve as bridges to mainstream demography and social science. The

1 We say “selectively” only to emphasize that these topics aren’t being recommended simply because they are new, but rather because they are important, well-vetted and fundamentally important. They happen to be new relative to the core concepts in evolutionary theory.

theories and methods for each of these areas are established and mathematically formalized (Cavalli-Sforza and Feldman 1981; Creanza, Kolodny, and Feldman 2017; Boyd and Richerson 1988; Derex and Mesoudi 2020; Mesoudi 2011) and can provide points-of-entry for classically trained demographers to frame their research in terms of evolutionary processes.

Culture

For examples specifically relevant to population growth, culturally transmitted values regarding son preferences have been modelled using a dual-inheritance framework (Bhattacharjya et al. 2008) and there are several models that specifically target low fertility preference (reviewed in Colleran 2016). Relatively little work has been done including these processes in population forecasts, many (but not all) of which assume a universal preference for a completed fertility of around two births per woman and that in time most countries have an average fertility very close to this (e.g., United Nations World Population Prospects 2019²). Newcomers to these ideas about cultural evolution and inheritance could refer to: (Richerson and Boyd 2008; Mesoudi 2011; Colleran 2016).

By including the full complement of factors that affect inter-generational transmission, comes the further emphasis that there is a great deal more to an evolutionary approach than isolating genetic mutations or focusing strictly on adaptation. Much evolutionary research focuses on social transmission, the processes of learning and teaching, and ways in which genes and environments interact across generations with application to crucial applied topics like persistent inequality in health (Wells 2016; Wells 2010; Kuzawa 2005; Thayer and Kuzawa 2014; Kuzawa and Sweet 2009) (also Wells this volume, Lawson and Gibson this volume). However, evolutionary research also helps resolve a range of important questions from what causes aging to where cognitive biases come from. The recommendation to embrace some of these newer areas of evolutionary thought is not limited to newcomers to evolutionary analysis; those already well-practiced with human evolutionary demography might also find ways to shed new light on old problems by examining cultural or epigenetic processes in their areas of interest.

Research in cultural evolution brings some of the nuance that someone only familiar with the (often problematic or flawed) studies in human evolutionary research that grab the headlines might find lacking. As one of us has pointed out (RS), many of the headline-grabbing problematic studies are flawed because they are overly deterministic (e.g., make simplistic arguments of the form: “men do X, women do Y, because evolution”) and lack acknowledgement of the obvious variation within- and between-populations that is typically the focus of much social science research (Sear 2020). Cultural evolutionary studies do not ignore the possibility of evolved species-typical traits; but they also acknowledge, and try to understand, how such traits interact with our social environment to produce behaviours and demographic outcomes. This greater incorporation of cultural evolutionary studies builds on the existing strengths in evolutionary demography and in human behavioural ecology, which considers how the environment shapes behaviours to produce within- and between- population variation in fitness relevant outcomes in our species (Cully and Shenk this volume, Blurton-Jones this volume, Hill this volume, Borgerhoff Mulder this volume). It is important to emphasise that cultural evolution and human behavioural ecology approaches to demography are able to help explain

2 https://population.un.org/wpp/Publications/Files/WPP2019_Highlights.pdf

contemporary variation in demographic patterns, since evolutionary approaches are sometimes misinterpreted to only encompass the study of human universals.

In a review of cultural evolutionary approaches to fertility decline, Colleran argued for more integration of cultural evolution into demography “as a means to develop multi-level models of fertility decline that emphasize the coevolution of economic and cultural change and not the a priori privileging of one over the other” (2016:2). Likewise, Creanza et al (2017:7786) put it rather matter-of-factly: “The literature on the interaction between cultural transmission and formal demography is quite sparse.” Cultural institutions, such as economic systems or education, are often treated as the “non-cultural” alternative to a hypothesis that fertility norms or biased transmission is responsible for fertility decline when in fact the institutions themselves and the values that drive them are also products of human cultural evolution (Colleran 2016). Another important insight from work on cumulative cultural evolution that is perhaps underappreciated in demography is that not only do cultural processes affect demographic behaviours but the structure of populations (size, age structure) affects the way cultural information accumulates and is transmitted (Derex and Mesoudi 2020). Further, cultural evolution is not just about inheritance, but includes the mechanisms and implications for social transmission among individuals both within and across generations (Bachrach 2013). It is worth noting that mainstream demography has also been criticised for inadequate incorporation of culture in its models (Petit and Charbit 2013), but also that some attempts to incorporate culture into so-far rather intractable demographic problems such as understanding variation in fertility have also considered evolutionary processes (the Theory of Conjunctural Action (Johnson-Hanks et al. 2011)), suggesting that both some mainstream and evolutionary demographers have come to similar conclusions about the importance of culture for demography.

Epigenetics

Another fascinating feature of this broader multi-faceted approach to the cross-generational transmission of information that affects human phenotypes is epigenetics. Epigenetic systems of inheritance involve molecular factors that affect how the genetic code is read or expressed.³ The molecular factors themselves can be inherited or may be physiological responses to stressful environmental conditions. While the way that epigenetic systems of inheritance function must surely be governed by genetic systems of inheritance, they make it possible for environmental signals to affect future generations by essentially turning genes on and off. This opens a pathway for the environment to affect some aspects of how traits manifest across generations without directly changing the underlying genes. Because the conditions experienced by a mother during or before pregnancy may affect the biology and physiology of her offspring and grand-offspring, there is a legacy effect of certain environmental factors that affects many outcomes relevant to demography, public health, and other fields (Kuzawa and Thayer 2011; Furrow, Christiansen, and Feldman 2013; Benyshek 2013). If these processes are not adequately understood, they could be inadvertently attributed to genetic factors because the changes can follow family lines if the factors that produce the signal triggering the epigenetic response are experienced persistently

3 The most recognizable form of epigenetics is that it makes it possible for cells to differentiate into different types as seen in bone cells and muscle cells and the like, which is accomplished by turning parts of the full DNA sequence on and off, but a more subtle version of this ‘turning on and off’ happens within and between generations and affects a range of factors from longevity to mental health.

across generations (Kuzawa and Sweet 2009). Numerous studies have shown enough empirical support for epigenetic pathways that a “proof-of-concept” is well established (see the study of the Dutch Hunger Winter by Heijmans et al (2008) for a well-known example). Associations between parental age and offspring health, a topic of interest in demography (Goisis et al. 2018), might be mediated by epigenetic effects (Markunas et al. 2016). However, a great deal more work could be done on the influence of epigenetics on demographic behaviour, as it is increasingly clear that these maternal signals from certain forms of stress, household effects, or parental age can be carried across generations.

A more nuanced understanding of the mechanisms of inheritance would be one very productive step forward for evolutionary demography, as well as a means of helping alleviate concerns with evolutionary approaches that are based on extremely problematic misapplication of evolutionary theory. How traits are transmitted between generations is widely misunderstood, in both the social sciences and evolutionary social sciences. Arguments about inheritance of traits are also misused, as “hereditarian” arguments about supposedly “genetic” group differences in traits such as intelligence seem to be on the rise again (Sear 2021). Increasing familiarity with, rather than closing the door on, the full suite of evolutionary processes will provide more effective tools to refute such studies. The genetic underpinnings of traits with relevance to human cognition, behaviour and demography are extremely complex, and are affected by a multiplicity of factors, including epigenetics, social determinants of health, and other gene-environment interactions, such as cultural evolution (Uchiyama, Spicer, and Muthukrishna 2020). An evolutionary demography that is able to develop and promote an appropriately nuanced understanding of the complexity of inheritance mechanisms would both be beneficial scientifically and might help dispel myths used to promote scientific racism and classism.

Appreciate the Classics

Second, in addition to (selectively) embracing the new, we recommend *appreciating the classic* as a means of continuing to advance evolutionary demography. In particular, human evolutionary demography would benefit from maintaining the key formative ideas from life history theory (sensu Charnov 1991; Charnov 1993; Stearns 1992; Roff 1993; Kozlowski 1992),⁴ population ecology (sensu Ginzburg and Colyvan 2004; Turchin 2003; MacArthur and Wilson 2001; May 1974; Roughgarden 1971), and where the two overlap (Abrams 1993; Reznick, Bryga, and Endler 1990; Fowler 1981). As Mace said in a 2014 article in *Demographic Research* “Biologists generally define evolutionary demography as the application of life history theory to population processes” (Mace 2014). Life history theory was initially practiced mostly by biologists but shares the same main endeavour as evolutionary demography: to apply evolutionary theory to demographic processes. However, contemporary human evolutionary demography has become at times detached from the main strengths of classical life history theory. Ideas that could use wider attention include using the principle of allocation to study trade-offs (Bolund 2020), the roles of population density and resources (Laskowski, Moiron, and Niemelä 2021),

4 This use of ‘life history theory’ exclusively refers to the original sense of the term originating in evolutionary biology and does not include the psychometric approaches used in some subfields of psychology, which have little to nothing to do with the theory developed in evolutionary biology (Sear 2020; Nettle and Frankenhuys 2019; Stearns and Rodrigues 2020).

more rigorous and theoretically grounded measures of fitness, and the use of formal analytical models (Jones and Bird 2014; Moorad and Nussey 2016). Life history theory and evolutionary ecology have used these things a lot, and still do, but we think there could be greater use of these classic techniques in human evolutionary demography.

Trade-offs and Energy Budgets

Formal models that incorporate energy budgets and trade-offs are central to classical life history theory. A highly influential example demonstrating how these concepts led to a deeper understanding of human life history evolution is Charnov's mammal life history model (1991; 1993). In it, Charnov takes an empirical finding as a given (the size of an offspring when it is energetically independent from its mother has a central tendency of about 1/3 of its mother's size) combined with the general shape of a growth curve that is typical of mammals and birds. He then derives a series of expressions that link demographic/life history traits together. Importantly, the model recreates known allometric patterns (traits like life span and age at first reproduction vary consistently with the adult size of an animal) and also articulates residuals from the average patterns across several demographic and physical characteristics; e.g., an animal with a larger than expected size at weaning will tend to have a later age at first birth, a longer lifespan, a slower growth rate, and a slower birth rate. Charnov's mammal model was tested a few years after its publication and held up extremely well in a cross-species study using high-quality life table data (Purvis and Harvey 1995) (the empirical evaluation in Purvis and Harvey (1995) also lends strong support for many of the central ideas in life history theory in general).

Having a theoretically explicit and mathematically formalized model articulating why biologists observed so much structure in demographic traits across species proved to be highly useful, and was extremely influential for several prominent evolutionary demographers and biological anthropologists (Jones 2011). Since its publication, Charnov's life history model (and related life history insights) has guided research on many topics, from why animals change size if they migrate from a continent to an island (Palkovacs 2003) to the relationships among a large "expensive" brain, slow growth, and long life in humans (Kuzawa et al. 2014). It was applied to primates and humans in what became the "life in the slow lane" approach to thinking about why primates are different from other mammals (Charnov and Berrigan 1993; Walker et al. 2006) (the "slow lane" refers to slower rates of growth and reproduction). In a thorough review of how life history theory explains the evolution of these canonical primate and human characteristics, Jones (2011:710) referred to the main question poised in Charnov and Berrigan (1993) ("Why do female primates live so long and have so few babies?") as "the central question for understanding primate life histories".

Indeed, the focus on trade-offs and cross-species analysis of primates and other animals recently led to a key observation regarding the human life history pattern. Human body growth is extremely slow on average from birth to maturity (humans have growth rates so low that they are closer to a boa constrictor than a mammal of similar size, Walker et al. (2006)) and has characteristic changes in velocity that occur during development. Human body growth slows down dramatically mid-childhood and stays low for a few years, a pattern that we do not see in other large primates. While many researchers had hypothesized that brain development might be responsible for the slowed body growth, the life history emphasis on trade-offs led

Kuzawa et al (2014) to study the energy metabolized during growth, using direct measures of glucose consumed by brain tissue, in humans, and compare that to changes in body growth. Indeed, they found that brains consume the most energy at about age 5 at a time when body growth is at its slowest and also found a clear inverse relationship between the rate of energy consumed by the brain and the rate of body growth across development. Showing that this trade-off, previously identified with cross-species comparisons, is so clearly evident in the physiological processing of glucose during development within one species, humans, was a major step forward and the culmination of years of research that was at least partly inspired by Charnov's mammal model. We still have a lot to learn about how these trade-offs affect human growth and development, and how evolutionary pressures moulded these responses across the evolution of mammals and primates.

Because Charnov's mammal model emphasizes the co-evolution of inter-related traits, anthropologists started thinking about ways that human patterns systematically differed from those of mammals and what this might tell us about how the evolution of some uniquely human characteristics.⁵ For example, the "grandmother hypothesis" appears several times in this volume (Tuljapurkar chapter, Dillon et al chapter). While this hypothesis has a few sub-variations, the main themes link the slow growth rates and extended periods of dependency that we observe among human children to a sexual division of activity and long post-reproductive life spans that were seen among adults in the foraging populations where these anthropologists worked (e.g., the Ache of Paraguay or the Hiwi of Venezuela or the Hadza of Tanzania; see Blurton-Jones Chapter and Hill Chapter). Identifying these relationships as an interesting and important demographic problem was inspired in part by Williams and Hamilton's work on senescence (Hamilton 1966; Williams 1957), but also by the theoretical framework provided by Charnov's mammal model (Hawkes et al. 1998).

Furthermore, the influential embodied capital theory of human evolution explains the link between the high-skill niche characteristic of human substance patterns, the complexity of human social interactions, and low adult mortality rates to the notably late-ages at which human foragers have their "peaks" in terms of ability to proficiently forage in complex environments (Kaplan and Robson 2002; Kaplan et al. 2000). The linkage of these different characteristics presented an interesting research problem because evolution tends to favour early and fast reproduction and studies of human foragers show that the most successful foragers, in terms of calories produced per unit time, were older individuals well beyond the ages of peak health and agility. It takes a long time to learn the skill needed to be a human forager and this extended learning time is so instrumental to our package of life history traits that mortality rates have to be extremely low relative to our nearest ancestors for this extended period of learning to pay off (this observation is important to models of cultural evolution as well, because childhood is an extended time of energetic dependence where a lot of social learning occurs). Part of the embodied capital approach suggests that the slow growth and brain development by children before adulthood, when they are fairly "bad" at getting their own food, is made possible by the excess production of older individuals (Lee Chapter). While a lot more could be said about the history of research on this topic and its anthropological relevance, our point here is that some

5 Perhaps not coincidentally, many of the early influential anthropologists working in this area overlapped with Charnov as graduate students or faculty at the University of Utah in the 1980s.

highly influential work on the human life history, and hence the evolution of demographic traits, was inspired by an elegant model that used trade-offs and mathematical formulation.

Population Density and Resources

Evolutionary approaches often include the role of ecological variation as a predictor of, or constraint on, change. Hence, they also highlight how variations in vital rates are influenced by social and ecological factors like population density, competition, and resource availability, all of which affect human populations. One of the first influential works in demography, Malthus' 1798 "Essay On the Principle of Population..." focused on exactly these issues, but — for understandable reasons — they have fallen out of favour in contemporary approaches of population. We suggest they could use more attention, with appropriate caution, in areas like projecting population sizes of the future.

Despite a relative lack of attention to these issues, a few classic works in demography have shown that population densities influence vital rates. For instance, Lutz et al (2006) showed that population density was negatively associated with fertility outcomes and preferences in a time series analysis of 145 countries. They recommended that population density be included in research on fertility determinants but did not mention population projections directly.

In an article that in many ways anticipated key strengths of evolutionary demography, Lee (1987) investigated density-dependence and homeostasis in historical data sets for Europe. This analysis was in part motivated by noticing the prominence of population density in animal ecology compared to its near absence in human demography. For countries with long time depth, Lee found a strong negative relationship between population density and income (detrended). For example, across Europe as a whole, he observed a statistically "large" effect of density on real wages and a clear sign of density-dependence on the ability of people to gain a key resource for the period from 1260 to 1840. The relationship between density and fertility was also negative. In the "modern world" Lee found that the nature of population homeostasis has changed as the constraints on growth are drastically different. When fertility is low and land has less of a constraint on economic growth, because inputs become less tied to photosynthesis and land area, constraints on growth are less tied to population density, but increasingly more tied to the actual availability of energy (Wrigley 2013).

Other historical analyses have found correlations between wages and population growth and other lines of evidence indicating density-dependence, with effects that weaken with the transition to fossil fuel economies (Wrigley 2013; Wrigley 1990; Kander, Malanima, and Warde 2014). The work of historical demographer Tony Wrigley showed that the demographic transition was associated with a large increase in inputs from fossil fuels and these change the way that land constrains growth and production (Wrigley 2013; Wrigley 1990). Once the use of coal became a major part of the English economy, relationships decoupled between population growth rate and consumables and between population growth rate and real wages, meaning that the nature of density dependence changed dramatically. In contemporary societies, many demographic traits correlate with energy availability at the national level (Burger, DeLong, and Hamilton 2011; DeLong, Burger, and Hamilton 2010), and such relationships are rarely if ever included in formal projections of future population size (Lee 2011).

The realization that density effects are different for post-industrial humans than in earlier times has led many to assume that they must not matter at all. The common dismissal of density

and ecological factors in demography probably has less to do with theoretical perspective than with the widely publicized predictions of impending disaster for humans that have not come to be but ignoring socio-ecological factors is ultimately short-sighted. The dismissal of density and ecological factors in demography may also be related to their politicisation: Malthus is read as a call to maintain the political status quo, and twentieth- and twenty-first-century concerns about rapid population growth and environmental degradation have been used to promote population control, at the expense of individual human rights. This potential for political misuse must absolutely be borne in mind in future research, alongside acknowledgement that there is little to be gained from making strong assumptions about specific fixed and static carrying capacities, but there is a great deal to be gained from understanding the mechanisms or pathways that alleviate density-dependent pressures or that change the way they operate (again, such mechanisms could and should be included in projections of population growth).

More abstractly, forecasters and social scientists generally need to realize that human populations have been growing for many generations and are far from an equilibrium state. The theoretical implications of human non-equilibrium dynamics is not at all well understood and rarely formally included in discussions of population growth (DeLong and Burger 2015; DeLong, Burger, and Hamilton 2010). Population forecasts commonly take for granted that a future equilibrium state exists (often that preference and behaviour will fix near two births per couple, globally), but the factors that draw us toward it, or those that interfere with density-dependent feedbacks, have not been thoroughly studied and applied in the area of population growth. Something as socially complicated as desired family size likely has inputs from many factors and these need to be understood before assuming a stasis and universal preference for the same value (Burger and DeLong 2016).

One of the reasons ecologists expect density to affect population dynamics, is that as population density increases, it will usually pass some threshold after which individuals in the population experience reduced access to a key resource. This kind of thinking has been used to address several questions of interest in ecology, such as what group sizes are optimal for different species or populations. Typically, there are benefits and costs to adding group members, such as reduced risk from predators up to a point where resources become limiting. Part of the human demographic relevance of population density is its effect on resources, but this is not the only reason for human demographers to be interested in population density (especially given humans have repeatedly shown they can change the exact relationship between population density and resources with technological innovation). Population density also affects social interactions and cumulative cultural evolution. As population size increases within a given area, density necessarily increases as well and density may interact with other factors, like mortality risk by age, or competition over favoured nesting/housing sites, or the nature and complexity of social hierarchies, or the number of cultural models one observes during childhood, or psychological mechanisms affected by the number of people, accidents, and deaths one observes in an urban setting which can skew one's own perception of risk. One of the mechanisms of cumulative cultural evolution is socially observing a wide range of social models for the reproduction and change of technologies or norms, as observing a greater variety of these in turn seems to spur more rapid innovation rates.

A modern understanding of energy, and the extra-somatic resources made possible by human cooperation, conflict, colonisation, and technological developments, could be essential

for resolving apparent tensions between Boserupian (technology and innovation focused) and Malthusian (constraint focused) approaches to thinking about and modelling population growth. Likewise, urbanization is such a key aspect of globalization and the near- to mid-term future of many human populations. Seeking general theory and approaches for how the changes that accompany urbanization affect demographic and social behaviour will be an increasingly important endeavour.

Better/Appropriate Measures of Fitness

Evolutionary demography could also focus on, and more-widely adopt, explicit and theoretically valid measures of fitness (McGraw and Caswell 1996, vanDaalen and Caswell this volume, Moorad this volume). This will not only improve rigour in the field but will also help move forward our understanding of the demographic transition. A great deal of evolutionary research in the human sciences uses proxy measures for fitness. Sometimes this is a matter of necessity as the data requirements of a good fitness measure can be hard to meet, but for all the conceptual centrality of fitness to evolutionary theory, it is not appropriately quantified near often enough. For example, we know stunningly little, even at the descriptive level, about changes in actual fitness during the demographic transition and such knowledge would be useful for both accurate description and explanation of the transition.⁶ We rarely have a detailed study of a valid measure of fitness applied to a long time series during the transition, nor do we have thorough understanding for how the components of fitness like child mortality and age at first birth change over time or how the strength of their correlation with fitness changes with time. This would help map out the timing and magnitude of fitness change or the correlations among fitness and its components (timing and number of births, survival, population growth rate).

The demographic transition is defined by reductions in fertility, that typically follow reductions in mortality, to very low levels resulting in populations that often have fertility levels below replacement. Many studies have looked at correlates of fitness but we know from evolutionary demography that such studies can be highly misleading, especially if changes in timing are one of the variables that can affect variation in fitness (McGraw and Caswell 1996). Variation in timing of the age at first birth is important for historical, evolutionary, and policy reasons, but the fitness implications of this cannot be understood using many common definitions of fitness that do not capture variation in timing. Likewise, the demographic transition is sometimes used to argue that human fertility behaviour is inherently sub-optimal or non-fitness maximizing. While this is certainly the outcome at the individual level in low-fertility contexts, for such an important topic there is a great deal to learn about whens, wheres, and hows of the fitness-aspects of the demographic transition and the individual- and

6 Two population-level quantities are especially likely to be used as fitness measures. One of them, r or the intrinsic rate of increase, tends to actually increase in the early part of the transition as mortality declines and only falls to pre-transition levels very late after fertility and mortality are both at very low levels. Another, NRR or the net reproductive rate, stays relatively flat (unchanging) through a large temporal swath of the middle of the transition. Neither of these capture within population variation in mean fitness, which is likely more important for explaining the impact of individual level decisions and behavioral responses to changing circumstances. The demographic transition is often referred to as something that is just 'bad' for fitness, and while we need to know a lot more than we do, we know there is a lot more to it than that.

group-level decisions and dynamics that co-occur with it. How various mechanisms of change are rate- or scale- dependent also needs more attention, as does the role of non-equilibrium dynamics. For example, what kinds of biological and cultural processes are especially relevant or irrelevant when change is so rapid and appears to be driven by individual adjustments to rapidly changing external circumstances?

For the demographic transition, ages of marriage and first reproduction change a lot and, importantly, neither age at first birth nor total fertility has a simple linear relationship with actual fitness. Individuals with the same reproductive success (total offspring produced) will have different fitness based on the timing of the births. The rate at which the population is growing and the fertility levels of the rest of the population also affect fitness. Linking back to earlier sections, there has been a resurgence of interest in the importance of population density on life history dynamics in evolutionary biology. Key to applying these insights to human evolutionary demography is an improved understanding of fitness (Dańko, Burger, and Kozłowski 2017; Dańko et al. 2018; Vries, Galipaud, and Kokko 2022). We need to know more about these relationships to simply have an adequate description of the demographic transition that would guide theory on how social/economic institutions interact to lead to the opportunities and perceptions behind the clearly non-fitness maximizing fertility decisions we see late in the transition. A dual-inheritance framework would help, by including cultural and genetic factors that affect fertility and mortality related decisions, but appropriate measures of fitness are needed as well. The case of more robust fitness measures and examples of their application can be found in these papers: McGraw and Caswell (1996); Korpelainen (2003); Jones and Bird (2014); Moorad (2013).

Many Benefits of an Evolutionary Approach

Some of the benefits of human evolutionary demography are not about adaptation. Likewise, evolutionary approaches apply to cases where non-adaptive behaviours seem common (like below replacement fertility). The focus on multiple levels of explanation and sources of variation can result in looking at a problem in a different way or may help guide questions that link mechanism and process to observed patterns. For example, an interest in how natural selection affects change in any given trait or behaviour requires an understanding of not just the mean or most typically observed, but of the variation as well. One reason for emphasizing the variance is that natural selection acts on heritable variation and if there is no heritable variation, there is a narrower range of phenotypes that can be modified across generations by differential fertility and mortality (Crow 1989). A second reason is that fitness is a relative measure. As such, understanding how evolutionary processes are affecting a given observed behaviour or physical characteristic depends on how it compares to the values (and associated strategies) of the rest of the population (e.g., a completed fertility of 3 is low if the population average is 6 but quite high if the population average is 1.5).

The emphasis on both the mean and variance present in many metrics designed to quantify evolutionary processes led two evolutionary demographers, including one of us (OB), to notice that studies of the fertility transition are often focused on changes in mean fertility while the variance is rarely discussed in detail (Hruschka and Burger 2016). They analysed variance in completed fertility across 72 low- and middle- income countries, emphasizing how variance changed as the mean declined, an important and overlooked topic, which was motivated by

an evolutionary approach. Yet, the findings of their analysis did not involve arguments about evolutionarily optimal fertility levels nor about changing allele frequencies, but were rather pragmatic and applied in nature. A lot of the variance in fertility among individuals is likely due to stochastic processes rather than to individual-level variables like wealth or education (91% of the samples they analysed were consistent with a Poisson process). This key finding suggests that there appear to be hard limits to how much of the variation in fertility can be explained by individual differences. Many studies of fertility at least implicitly assume that most of the variation in fertility behaviour among individuals is explainable with variables of the sort typically used in regression analysis (education, family size, wealth, media exposure, etc), when a lot of this variance may be inaccessible to such measures (if the underlying process is indeed consistent with a Poisson counting process). Moreover, the relative importance of individual-level variables was likely greater at low levels of fertility than at medium or high levels, which is again probably not the kind of finding that social scientists would typically associate with “an evolutionary approach”, but is indicative of the strength of the multi-disciplinary and multi-level approach of human evolutionary demography. Indeed, most of the results of this analysis were “applied” in nature and of high practical relevance to public health and demography with seemingly little to do, at the surface level, with explanations of how fertility patterns evolved. That is, the benefits came from the framing of the question rather than a quest to find an adaptive explanation for an observed trend.

Melting Dichotomies with Evolutionary Demography

In these Closing Thoughts, we are emphasizing some strengths of evolutionary demography and suggesting some paths forward to help achieve further integration between social and evolutionary sciences. The combinations of the emphasis of evolutionary demography on multiple levels of explanation and interdisciplinary nature combined with realizations that multiple processes influence phenotypic change, that the role of culture can be explicitly modelled and analysed, and that non-adaptive perspectives are both possible and common, lead to the melting of several long-held structural dichotomies that have served to hold research back.

Many dichotomies end up converging on an answer that takes some form of “a bit of both”. By incorporating contemporary understanding of heritability one such dichotomy that dissolves into “a bit of both” is nature vs. nurture. Research in cultural transmission and epigenetics has demonstrated that traits that are strictly one or the other are exceedingly rare. Inclusion of understandings of cultural transmission and epigenetics could further dissolve many of the problematic issues that come from placing nature and nurture in opposition to each other while also identifying the mechanisms for how the genetic and biological interact with and are part of the social and the learned. Another dichotomy that disappears is that between structural and ideational explanations of the demographic transition. With a contemporary understanding of evolutionary processes, it is difficult to claim that the demographic transition could be all large-scale macro-economic drivers. However, it is perhaps even less tenable to claim that it is totally driven by norms spread by television and/or imitation of behaviours one observes in their neighbourhood. The economic circumstances, the actual and perceived trade-offs for investing in capital, and the processes of innovation and imitation that underlie cultural transmission of fertility norms are inter-connected. A modern science of cultural evolution

that includes attention to trade-offs recognizes both of these factors. A third dichotomy that the recommendations here can help dissolve is that between Boserupian and Malthusian processes of population growth. Do population processes drive innovations that lead to technological developments that in turn relieve population pressures? Yes, of course. Are population growth rates and sizes ultimately governed by finite resource structures? Yes, of course. Both are true. The challenge is not letting an interest in one of the processes, often driven by the scale of a question or the dataset to which it is applied, lead to the denial of the other.⁷

Traditional and evolutionary demography need one another. In our view, one of the negative perceptions of any field with “evolutionary” in the name derives from the worst instances of attempted evolutionary analysis that often seem to get the most press (to be clear, this describes a minority of evolutionary research). Such studies are based on rather hackneyed post-hoc adaptive explanations, poorly designed sampling strategies, occasionally even obviously political motivation, or all three. Most evolutionary research is not like that. It is increasingly clear to us that an eyeroll or snarky tweet is not sufficient response to this minority of evolutionary research, which continues to do so much damage to the attempts of many researchers to cross the evolutionary-social science boundary. So, two additional recommendations we have for evolutionary demographers, and other evolutionary social sciences, are (i) to take much more active steps to improve rigour in the evolutionary field, and (ii) to continue to break through disciplinary walls by finding points of overlap among evolutionary and social science perspectives that strengthen both science and policy. The Chapters in this volume provide excellent examples for both of these points.

Across these dissolved dichotomies are many opportunities to advance research and understanding of a variety of topics. Certainly, the modelling of population growth and the components that contribute to it are strong contenders for areas that could be improved with more input from multiple-levels of explanation and dynamic models informed by theory. But many other topics, from persistent inequality to wealth disparity to family planning, that are reasonably considered as fundamental demographic topics could be advanced with the nuanced perspectives presented by the chapters of this volume. Indeed, in today’s world, approaches that have the potential to dissolve dichotomies or reduce polarization are much needed across sectors of science, policy, and elsewhere.

References⁸

- Abrams, Peter A. 1993. ‘Does Increased Mortality Favor the Evolution of More Rapid Senescence?’, *Evolution*, 47.3: pp. 877–87, <https://doi.org/10.2307/2410191>
- Bachrach, Christine A. 2013. ‘Culture and Demography: From Reluctant Bedfellows to Committed Partners’, *Demography*, 51.1: pp. 3–25, <https://doi.org/10.1007/s13524-013-0257-6>
- Benyshek, Daniel C. 2013. ‘The “Early Life” Origins of Obesity-Related Health Disorders: New Discoveries Regarding the Intergenerational Transmission of Developmentally Programmed Traits in the Global

7 From the great demographer Wrigley: “There is an important sense in which the problem identified by the classical economists remains with us today since, as long as fossil fuels provide the bulk of the energy consumed in advanced economies, difficulties are postponed rather than indefinitely set aside.”

8 Note this chapter has been posted on the Open Science Framework website since 26/02/2022, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

- Cardiometabolic Health Crisis', *American Journal of Physical Anthropology*, 152.S57: pp. 79–93, <https://doi.org/10.1002/ajpa.22393>
- Bhattacharjya, Debarun, Anant Sudarshan, Shripad Tuljapurkar, Ross Shachter, and Marcus Feldman. 2008. 'How Can Economic Schemes Curtail the Increasing Sex Ratio at Birth in China?', *Demographic Research*, 19.54: pp. 1831–50, <https://doi.org/10.4054/demres.2008.19.54>
- Bolund, Elisabeth. 2020. 'The Challenge of Measuring Trade-Offs in Human Life History Research', *Evolution and Human Behavior*, 41.6 (Special issue: Current Debates in Human Life History Research edited by Willem Frankenhuis and Daniel Nettle): pp. 502–12, <https://doi.org/10.1016/j.evolhumbehav.2020.09.003>
- Bongaarts, John, and Susan C. Watkins. 1996. 'Social Interactions and Contemporary Fertility Transitions', *Population and Development Review*, 22.4: pp. 639–82, <https://doi.org/10.2307/2137804>
- Boyd, Robert, and Peter J. Richerson. 1988. *Culture and the Evolutionary Process* (Chicago: University of Chicago press).
- Burger, Oskar, and John P. DeLong. 2016. 'What If Fertility Decline Is Not Permanent? The Need for an Evolutionarily Informed Approach to Understanding Low Fertility', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371.1692: p. 20150157, <https://doi.org/10.1098/rstb.2015.0157>
- Burger, Oskar, John P. DeLong, and Marcus J. Hamilton. 2011. 'Industrial Energy Use and the Human Life History', *Scientific Reports*, 1.1: pp. 1–7, <https://doi.org/10.1038/srep00056>
- Cavalli-Sforza, Luigi Luca, and Marcus W. Feldman. 1981. *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton: Princeton University Press).
- Charnov, Eric L. 1991. 'Evolution of Life History Variation among Female Mammals', *Proceedings of the National Academy of Sciences*, 88.4: pp. 1134–37, <https://doi.org/10.1073/pnas.88.4.1134>
- . 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology* (New York: Oxford University Press), VI.
- Charnov, Eric L., and David Berrigan. 1993. 'Why Do Female Primates Have Such Long Lifespans and so Few Babies? Or Life in the Slow Lane', *Evolutionary Anthropology: Issues, News, and Reviews*, 1.6: pp. 191–94, <https://doi.org/10.1002/evan.1360010604>
- Cleland, John, and Christopher Wilson. 1987. 'Demand Theories of the Fertility Transition: An Iconoclastic View', *Population Studies*, 41.1: pp. 5–30, <https://doi.org/10.1080/0032472031000142516>
- Colleran, Heidi. 2016. 'The Cultural Evolution of Fertility Decline', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371.1692: p. 20150152, <https://doi.org/10.1098/rstb.2015.0152>
- Creanza, Nicole, Oren Kolodny, and Marcus W. Feldman. 2017. 'Cultural Evolutionary Theory: How Culture Evolves and Why It Matters', *Proceedings of the National Academy of Sciences*, 114.30: pp. 7782–89, <https://doi.org/10.1073/pnas.1620732114>
- Crow, James F. 1989. 'Update to "Some Possibilities for Measuring Selection Intensities in Man"', *Human Biology*, 61.5/6: pp. 763–75. <https://www.jstor.org/stable/41478723>
- Dańko, Maciej J., Oskar Burger, Krzysztof Argasiński, and Jan Kozłowski. 2018. 'Extrinsic Mortality Can Shape Life-History Traits, Including Senescence', *Evolutionary Biology*, 45.4: pp. 395–404, <https://doi.org/10.1007/s11692-018-9458-7>
- Dańko, Maciej Jan, Oskar Burger, and Jan Kozłowski. 2017. 'Density-Dependence Interacts with Extrinsic Mortality in Shaping Life Histories', *PLoS One*, 12.10: p. e0186661, <https://doi.org/10.1371/journal.pone.0186661>
- DeLong, John P., and Oskar Burger. 2015. 'Socio-Economic Instability and the Scaling of Energy Use with Population Size', *PLoS One*, 10.6: p. e0130547, <https://doi.org/10.1371/journal.pone.0130547>
- DeLong, John P., Oskar Burger, and Marcus J. Hamilton. 2010. 'Current Demographics Suggest Future Energy Supplies Will Be Inadequate to Slow Human Population Growth', *PLoS One*, 5.10: p. e13206, <https://doi.org/10.1371/journal.pone.0013206>

- Derex, Maxime, and Alex Mesoudi. 2020. 'Cumulative Cultural Evolution within Evolving Population Structures', *Trends in Cognitive Sciences*, 24.8: pp. 654–67, <https://doi.org/10.1016/j.tics.2020.04.005>
- Fowler, Charles W. 1981. 'Density Dependence as Related to Life History Strategy', *Ecology*, 62.3: pp. 602–10, <https://doi.org/10.2307/1937727>
- Furrow, Robert E., Freddy B. Christiansen, and Marcus W. Feldman. 2013. 'Epigenetic Variation, Phenotypic Heritability, and Evolution', in *Epigenetics and Complex Traits* ed. by Anna K. Naumova, and Celia M. T. Greenwood (New York: Springer), pp. 233–46, https://doi.org/10.1007/978-1-4614-8078-5_10
- Ginzburg, Lev, and Mark Colyvan. 2004. *Ecological Orbits: How Planets Move and Populations Grow* (Oxford and New York: Oxford University Press).
- Goisis, Alice, Hanna Remes, Kieron Barclay, Pekka Martikainen, and Mikko Myrskylä. 2018. 'Paternal Age and the Risk of Low Birth Weight and Preterm Delivery: A Finnish Register-Based Study', *J Epidemiol Community Health*, 72.12: pp. 1104–09, <https://doi.org/10.1136/jech-2017-210170>
- Hamilton, William D. 1966. 'The Moulding of Senescence by Natural Selection', *Journal of Theoretical Biology*, 12.1: pp. 12–45, [https://doi.org/10.1016/0022-5193\(66\)90184-6](https://doi.org/10.1016/0022-5193(66)90184-6)
- Hawkes, K., J. F. O'Connell, N. G. Blurton Jones, H. Alvarez, and E. L. Charnov. 1998. 'Grandmothering, Menopause, and the Evolution of Human Life Histories', *Proceedings of the National Academy of Sciences*, 95.3: pp. 1336–39, <https://doi.org/10.1073/pnas.95.3.1336>
- Heijmans, Bastiaan T., Elmar W. Tobi, Aryeh D. Stein, and others. 2008. 'Persistent Epigenetic Differences Associated with Prenatal Exposure to Famine in Humans', *Proceedings of the National Academy of Sciences*, 105.44: pp. 17046–17049, <https://doi.org/10.1073/pnas.0806560105>
- Henrich, Joseph, and Richard McElreath. 2007. 'Dual-Inheritance Theory: The Evolution of Human Cultural Capacities and Cultural Evolution', In *Oxford Handbook of Evolutionary Psychology*, ed. by Louise Barrett, and Robin Dunbar (Oxford: Oxford University Press), <https://doi.org/10.1093/oxfordhb/9780198568308.013.0038>
- Hruschka, Daniel J., and Oskar Burger. 2016. 'How Does Variance in Fertility Change over the Demographic Transition?', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371.1692: p. 20150155, <https://doi.org/10.1098/rstb.2015.0155>
- Jablonka, Eva, and Marion J. Lamb. 2014. *Evolution in Four Dimensions Revised Edition: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life* (Cambridge, Massachusetts: MIT Press).
- Johnson-Hanks, Jennifer A., Christine A. Bachrach, S. Philip Morgan, and Hans-Peter Kohler. 2011. 'The Theory of Conjunctural Action', In *Understanding Family Change and Variation* (Dordrecht: Springer), pp. 1–22, https://doi.org/10.1007/978-94-007-1945-3_1
- Jones, James Holland, and Rebecca Bliege Bird. 2014. 'The Marginal Valuation of Fertility', *Evolution and Human Behavior*, 35.1: pp. 65–71, <https://doi.org/10.1016/j.evolhumbehav.2013.10.002>
- Jones, James Holland. 2011. 'Primates and the Evolution of Long, Slow Life Histories', *Current Biology*, 21.18: pp. R708–R717, <https://doi.org/10.1016/j.cub.2011.08.025>
- Kander, Astrid, Paolo Malanima, and Paul Warde. 2014. *Power to the People: Energy in Europe over the Last Five Centuries* (Princeton: Princeton University Press).
- Kaplan, Hillard, Kim Hill, Jane Lancaster, and A. Magdalena Hurtado. 2000. 'A Theory of Human Life History Evolution: Diet, Intelligence, and Longevity', *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 9.4: pp. 156–85, [https://doi.org/10.1002/1520-6505\(2000\)9:4<156::aid-evan5>3.0.co;2-7](https://doi.org/10.1002/1520-6505(2000)9:4<156::aid-evan5>3.0.co;2-7)
- Kaplan, Hillard S., and Arthur J. Robson. 2002. 'The Emergence of Humans: The Coevolution of Intelligence and Longevity with Intergenerational Transfers', *Proceedings of the National Academy of Sciences*, 99.15: pp. 10221–10226, <https://doi.org/10.1073/pnas.152502899>
- Korpelainen, Helena. 2003. 'Human Life Histories and the Demographic Transition: A Case Study from Finland, 1870–1949', *American Journal of Physical Anthropology*, 120.4: pp. 384–90, <https://doi.org/10.1002/ajpa.10191>

- Kozłowski, Jan. 1992. 'Optimal Allocation of Resources to Growth and Reproduction: Implications for Age and Size at Maturity', *Trends in Ecology & Evolution*, 7.1: pp. 15–19, [https://doi.org/10.1016/0169-5347\(92\)90192-e](https://doi.org/10.1016/0169-5347(92)90192-e)
- Kuzawa, Christopher W. 2005. 'Fetal Origins of Developmental Plasticity: Are Fetal Cues Reliable Predictors of Future Nutritional Environments?', *American Journal of Human Biology*, 17.1: pp. 5–21, <https://doi.org/10.1002/ajhb.20091>
- Kuzawa, Christopher W., Harry T. Chugani, Lawrence I. Grossman, and others. 2014. 'Metabolic Costs and Evolutionary Implications of Human Brain Development', *Proceedings of the National Academy of Sciences*, 111.36: pp. 13010–13015, <https://doi.org/10.1073/pnas.1323099111>
- Kuzawa, Christopher W., and Elizabeth Sweet. 2009. 'Epigenetics and the Embodiment of Race: Developmental Origins of US Racial Disparities in Cardiovascular Health', *American Journal of Human Biology*, 21.1: pp. 2–15, <https://doi.org/10.1002/ajhb.20822>
- Kuzawa, Christopher W., and Zaneta M. Thayer. 2011. 'Timescales of Human Adaptation: The Role of Epigenetic Processes', *Epigenomics*, 3.2: pp. 221–34, <https://doi.org/10.2217/epi.11.11>
- Laland, Kevin N., Tobias Uller, Marcus W. Feldman, and others. 2015. 'The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions', *Proceedings of the Royal Society B: Biological Sciences*, 282.1813: p. 20151019, <https://doi.org/10.1098/rspb.2015.1019>
- Laskowski, Kate L., Maria Moiron, and Petri T. Niemelä. 2021. 'Integrating Behavior in Life-History Theory: Allocation versus Acquisition?', *Trends in Ecology & Evolution*, 36.2: pp. 132–38, <https://doi.org/10.1016/j.tree.2020.10.017>
- Lee, Ronald. 2011. 'The Outlook for Population Growth', *Science*, 333.6042: pp. 569–73, <https://doi.org/10.1126/science.1208859>
- Lee, Ronald D. 1987. 'Population Dynamics of Humans and Other Animals', *Demography*, 24.4: pp. 443–65, <https://doi.org/10.2307/2061385>
- Lutz, Wolfgang, Maria Rita Testa, and Dustin J. Penn. 2006. 'Population Density Is a Key Factor in Declining Human Fertility', *Population and Environment*, 28.2: pp. 69–81, <https://doi.org/10.1007/s11111-007-0037-6>
- MacArthur, Robert H., and Edward O. Wilson. 2001. *The Theory of Island Biogeography* (Princeton: Princeton university press), I.
- Mace, Ruth. 2014. 'When Not to Have Another Baby: An Evolutionary Approach to Low Fertility', *Demographic Research*, 30: pp. 1074–96. <https://doi.org/10.4054/demres.2014.30.37>
- Markunas, Christina A., Allen J. Wilcox, Zongli Xu, and others. 2016. 'Maternal Age at Delivery Is Associated with an Epigenetic Signature in Both Newborns and Adults', *PLoS ONE*, 11.7: p. e0156361, <https://doi.org/10.1371/journal.pone.0156361>
- May, Robert M. 1974. 'Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos', *Science*, 186.4164: pp. 645–47, <https://doi.org/10.1126/science.186.4164.645>
- McGraw, James B., and Hal Caswell. 1996. 'Estimation of Individual Fitness from Life-History Data', *The American Naturalist*, 147.1: pp. 47–64, <https://doi.org/10.1086/285839>
- Mesoudi, Alex. 2011. *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences* (Chicago: University of Chicago Press).
- Moorad, Jacob A. 2013. 'A Demographic Transition Altered the Strength of Selection for Fitness and Age-Specific Survival and Fertility in a 19th Century American Population', *Evolution*, 67.6: pp. 1622–34, <https://doi.org/10.1111/evo.12023>
- Moorad, Jacob A., and Daniel H. Nussey. 2016. 'Evolution of Maternal Effect Senescence', *Proceedings of the National Academy of Sciences*, 113.2: pp. 362–67, <https://doi.org/10.1073/pnas.1520494113>
- Nettle, Daniel, and Willem E. Frankenhuis. 2019. 'The Evolution of Life-History Theory: A Bibliometric Analysis of an Interdisciplinary Research Area', *Proceedings of the Royal Society B: Biological Sciences*, 286.1899: p. 20190040, <https://doi.org/10.1098/rspb.2019.0040>

- Palkovacs, Eric P. 2003. 'Explaining Adaptive Shifts in Body Size on Islands: A Life History Approach', *Oikos*, 103.1: pp. 37–44, <https://doi.org/10.1034/j.1600-0706.2003.12502.x>
- Petit, Véronique, and Yves Charbit. 2013. 'The French School of Demography: Contextualizing Demographic Analysis', *Population and Development Review*, 38.S1: pp. 322–33, <https://doi.org/10.1111/j.1728-4457.2013.00567.x>
- Purvis, A., and P. H. Harvey. 1995. 'Mammal Life-History Evolution: A Comparative Test of Charnov's Model', *Journal of Zoology*, 237.2: pp. 259–83, <https://doi.org/10.1111/j.1469-7998.1995.tb02762.x>
- Reznick, David A., Heather Bryga, and John A. Endler. 1990. 'Experimentally Induced Life-History Evolution in a Natural Population', *Nature*, 346.6282: pp. 357–59, <https://doi.org/10.1038/346357a0>
- Richerson, Peter J., and Robert Boyd. 2008. *Not by Genes Alone: How Culture Transformed Human Evolution* (Chicago: University of Chicago press).
- Roff, Derek. 1993. *Evolution of Life Histories: Theory and Analysis* (New York: Springer).
- Roughgarden, Jonathan. 1971. 'Density-Dependent Natural Selection', *Ecology*, 52.3: pp. 453–68, <https://doi.org/10.2307/1937628>
- Sear, Rebecca. 2020. 'Do Human 'Life History Strategies' Exist?', *Evolution and Human Behavior*, 41.6: pp. 513–26, <https://doi.org/10.1016/j.evolhumbehav.2020.09.004>
- . 2021. 'Demography and the Rise, Apparent Fall, and Resurgence of Eugenics', *Population Studies*, 75.sup1: pp. 201–20, <https://doi.org/10.1080/00324728.2021.2009013>
- Stearns, Stephen C. 1992. *The Evolution of Life Histories* (Oxford, New York: Oxford University Press).
- Stearns, Stephen C., and António M. M. Rodrigues. 2020. 'On the Use of "Life History Theory" in Evolutionary Psychology', *Evolution and Human Behavior*, 41.6: pp. 474–85, <https://doi.org/10.1016/j.evolhumbehav.2020.02.001>
- Thayer, Zaneta M., and Christopher W. Kuzawa. 2014. 'Early Origins of Health Disparities: Material Deprivation Predicts Maternal Evening Cortisol in Pregnancy and Offspring Cortisol Reactivity in the First Few Weeks of Life', *American Journal of Human Biology*, 26.6: pp. 723–30, <https://doi.org/10.1002/ajhb.22532>
- Turchin, Peter (eds.). 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis* (Princeton: Princeton university press), XXXV.
- Uchiyama, Ryutaro, Rachel Spicer, and Michael Muthukrishna. 2020. 'Cultural Evolution of Genetic Heritability', *Behavioral and Brain Sciences*, 45. <https://doi.org/10.1017/s0140525x21000893>
- Vries, Charlotte de de, Matthias Galipaud, and Hanna Kokko. 2022. 'Extrinsic Mortality and Senescence: A Guide for the Perplexed', *bioRxiv*, <https://doi.org/10.1101/2022.01.27.478060>
- Walker, Robert, Kim Hill, Oskar Burger, and A. Magdalena Hurtado. 2006. 'Life in the Slow Lane Revisited: Ontogenetic Separation between Chimpanzees and Humans', *American Journal of Physical Anthropology*, 129.4: pp. 577–83, <https://doi.org/10.1002/ajpa.20306>
- Wells, Jonathan 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: pp. 1–17, <https://doi.org/10.1002/ajhb.20994>
- . 2016. *The Metabolic Ghetto: An Evolutionary Perspective on Nutrition, Power Relations and Chronic Disease* (Cambridge: Cambridge University Press).
- Williams, George C. 1957. 'Pleiotropy, Natural Selection, and the Evolution of Senescence', *Evolution*, 11.4: pp. 398–411, <https://doi.org/10.2307/2406060>
- Wrigley, Edward Anthony. 1990. *Continuity, Chance and Change: The Character of the Industrial Revolution in England* (Cambridge: Cambridge University Press).
- . 2013. 'Energy and the English Industrial Revolution', *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 371.1986: p. 20110568, <https://doi.org/10.1098/rsta.2011.0568>