

2 Life History

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2.1 Introduction

A life history describes the timing and duration of key demographic events – like gestation, birth, reproduction, and death – and also rates of physiological processes such as growth, development, and aging (Figure 2.1). All species' life histories are unique, and so what does it mean to reflect upon the uniqueness of our own species? Humans are indeed curious creatures. We have big brains and develop slowly with a long juvenile period with novel stages of childhood and adolescence. We live long postreproductive life spans and cooperate extensively in a multigenerational network, whereby kin and nonkin help subsidize female reproduction (see Chapters 5, 6, 12, and 13). Biparental care, and aid from grandparents, adult siblings, other kin, and neighbors are vital. Human children soak up information from others and creatively adapt and innovate new cultures and technologies. Learning and skill development, combined with cooperative acquisition and distribution, enables complex subsistence strategies targeting high-quality, nutrient-dense foods. This bundle of demographic and socioeconomic traits comprises the Human Adaptive Complex (Kaplan et al. 2010), whose origin, maintenance, and variable expression has generated much discussion and controversy, and a growing body of empirical studies.

Theories that are too human-specific may be criticized for their limited generalizability or utility in the biological sciences, in the same way that defining culture to include language and other human traits limits the ability to ever study culture in nonhumans. One way of defining uniqueness is to compare traits among species with shared phylogenetic history. Humans are mammals, primates, and hominins. So we can ask how the life history of humans differs from that of other mammals, primates, and hominins. Comparisons with our nearest relatives, wild chimpanzees and bonobos, offer important insights, as these are believed to have a life history similar to our last common ancestor from 7–10 million years ago (Wrangham 1987). Compared to humans, our chimpanzee cousins have shorter lives, smaller brains, and bodies that grow and develop more rapidly. Another approach is to assess whether human traits are outside the range expected for a comparably sized mammal or primate. Given allometric (or scaling) relationships of many physiological processes and traits with body size, we can assess uniqueness by taking our species-typical body size into account.

This chapter introduces life history theory (LHT) and applies it to understanding the evolution of the human life course. The perspective I take serves to illustrate the

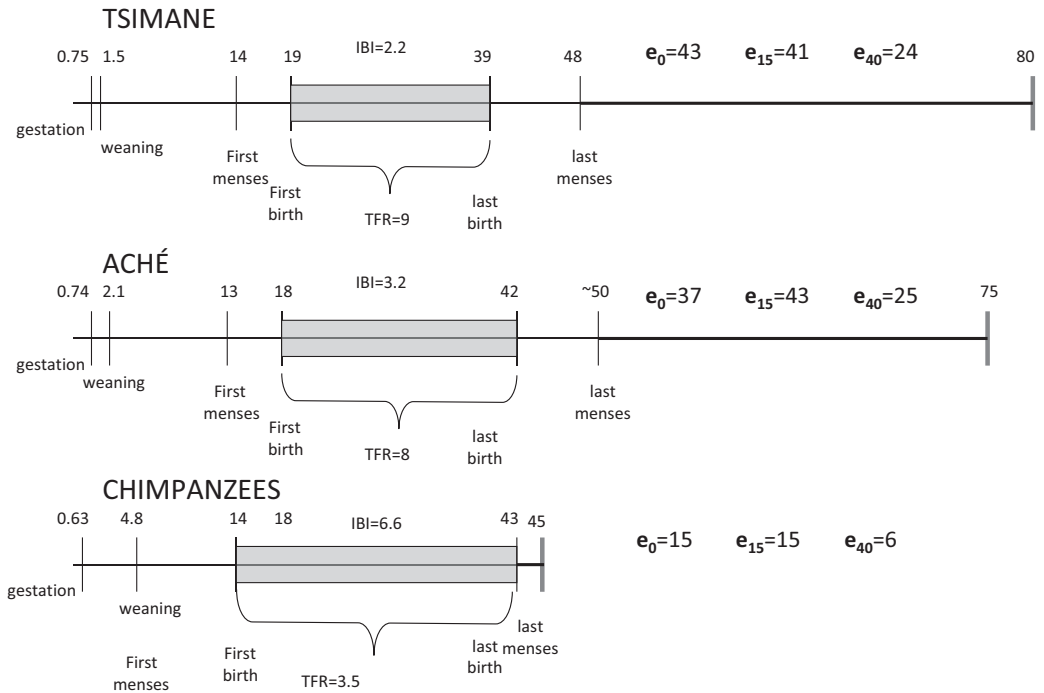


Figure 2.1 Comparative life histories of humans and chimpanzees. Aché data from Hill and Hurtado (1996), Tsimane data from Gurven et al. (2007). Chimpanzee mortality data from Gurven and Gomes (2017). Maximum life span is defined as age X , where survivorship $L_X = 0.05$.

broad utility of a life history framework for studying human variability, and so cannot possibly cover all areas of study. Section 2.2 reviews the history of LHT in the evolutionary social sciences. Section 2.3 synthesizes theoretical and empirical approaches toward understanding the Human Adaptive Complex, focusing primarily here on postreproductive life span. Section 2.4 discusses applications of LHT to understanding variation among humans, focusing on demographic, physiological, and psychological traits. Finally, Section 2.5 highlights several unresolved issues and future directions.

2.2 Life History Theory as a Theoretical Framework

2.2.1 What Is Life History Theory?

Life history theory studies the diversity of life history “strategies” across species that have been shaped by natural selection. While core ideas of life history theory can be traced back to Darwin and R. A. Fisher, Lamont Cole’s 1954 paper “The population consequences of life history phenomena” presented the first mathematical formulation for evaluating fitness consequences of variation in life history traits. LHT soon developed largely from evolutionary biology and population ecology (see Roff (1993)



Figure 2.2 The human life cycle. Infancy, childhood, adolescence, adulthood, grandparenthood. Central to the evolved human life history is the transfer of food, aid, information, and other resources within and among generations. Photos credit: Michael Gurven.

and Stearns (1992)), with human applications appearing by the 1980s. Life history strategies reflect the timing and duration of key life cycle components that can affect biological fitness. The life cycle includes gestation, birth, juvenility, maturation, reproduction, senescence, and death (Figure 2.2). Related traits derived from this cycle include size at birth and at sexual maturity, adult life span, number and size of offspring, and length of interbirth intervals.

The idea of an optimal life history is best illustrated by considering the hypothetical “Darwinian Demon” – an organism that reproduces immediately after being born, then produces unlimited offspring over an infinitely long life span. That no such organism could exist confirms the inability to maximize all fitness components simultaneously, and the importance of trade-offs given limited time, effort, and energy. Energy allocated to one function cannot be spent on others, and hence the optimal allocations among growth, reproduction, and maintenance functions favored by natural selection result in a species’ life history (Figure 2.3). A major trade-off early in life is between growth and reproduction, where growth affects future production, reproduction, and survival. Another way to frame this trade-off is between current and future reproduction, often identified as the *cost of reproduction* (see Section 2.4.3). In general, this trade-off results in greater reproductive effort with

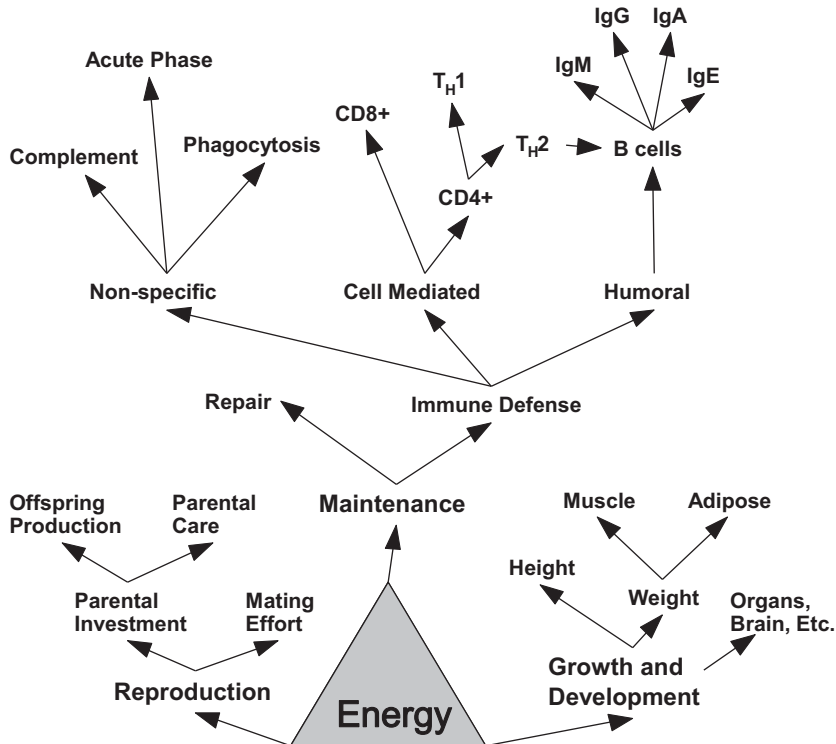


Figure 2.3 Life history trade-offs. Energy is allocated to somatic growth and development, reproduction, and somatic maintenance. Each of these three macro-categories contains multiple suballocation decisions. Adapted from Blackwell (2009).

age among adults, as the diminishing shadow of the future reduces the cost of reproduction (this idea has been called the terminal investment hypothesis). While trade-offs in the face of energetic limitation represent the bread and butter of LHT, empirical evaluation of trade-offs can be tricky if individuals vary in budget size and other constraints, a problem often identified as “phenotypic correlation” (see Box 2.1).

One of the fundamental insights of LHT is that mortality is the prime sculptor of life history pace and investments. More precisely, *exogenous* mortality – that is, deaths due to age- and condition-independent causes – affects trade-offs between present and future decisions and consequences. Although the concept of exogenous mortality may be problematic due to its unrealistic partitioning of causes of death, its heuristic value permits a convenient starting point for modeling trait evolution. High exogenous mortality puts a premium on stopping or accelerating growth, earlier reproduction, and less maintenance (i.e., more rapid aging and shorter life span). Low exogenous mortality promotes slower growth and larger body size (when fecundity is size-dependent), slower aging due to higher investments in maintenance, and hence longer life span. This chief insight, often credited to Williams (1957), is usually stated as a universal principle rather than as a prediction specific

Box 2.1 Challenge of Phenotypic Correlations

An ideal way to assess a life history trade-off is to experimentally induce a change in one phenotypic trait, and/or in energy budgets, and measure a causal response in the focal trait of interest. However, randomized sample selection and experimental manipulation are practically, and often ethically, difficult obstacles when working with humans. Many human studies instead use cross-sectional, observational designs. While convenient, these usually lack the ability to make strong causal inferences and are fraught with “phenotypic correlations” (referred to as self-selection or endogeneity in other disciplines). For example, individuals in better condition may both live longer and can afford to support more children, resulting in a spurious positive relationship between survivorship and fertility, instead of the negative trade-off suggested by the cost of reproduction. Alternatively, a predicted inverse relationship may be revealed by such analysis, but may not reflect actual trade-offs. Figure B2.1.1 shows the expected inverse relationship between total fertility rate (*TFR*) and life expectancy (e_0) across 183 countries. However, countries with high e_0 are wealthier, and a country’s wealth reflects higher-quality investments in schooling and fewer children. The “true” relationship between fertility and life expectancy is thus confounded by wealth and other factors.

One method for handling phenotypic correlations involves using multivariate statistics to adjust for the self-selected differences in condition. In the example previously, we can add covariates that might otherwise account for a potentially spurious relationship between e_0 and *TFR*. Including per capita

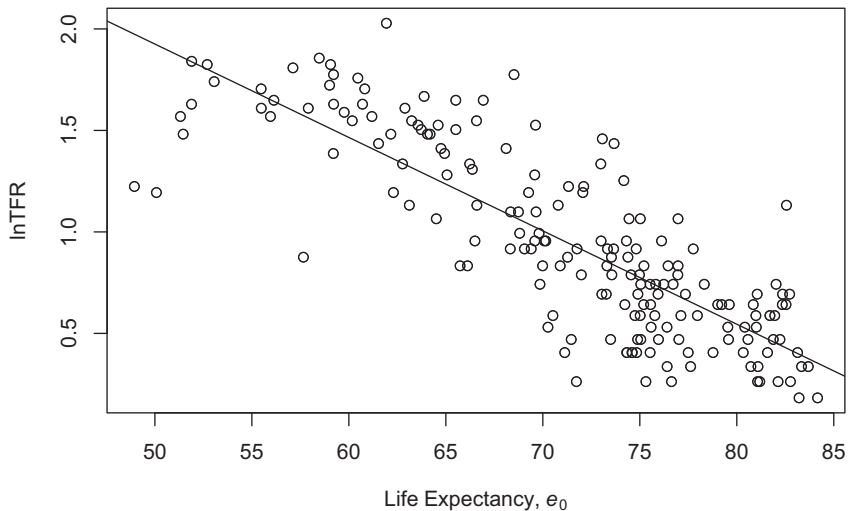


Figure B2.1.1 Relationship between total fertility rate (*TFR*) and life expectancy (e_0) in 183 countries. Data source: Human Development Report 2015.

Table B2.1.1 Regression of fertility (lnTFR) on life expectancy (e_0).

Variables included in regression	b (for e_0)	Std. β	p	Adj R^2
e_0	-0.046	-0.82	<0.0001	0.67
+ln GNP	-0.031	-0.55	<0.0001	0.72
+ln GNP, ln MMR	-0.018	-0.32	<0.0001	0.74
+ln GNP, ln MMR, education index	-0.017	-0.30	<0.0002	0.75
+ln GNP, ln MMR, education index, Gini index	-0.011	-0.20	0.025	0.77

Parameter estimates from the regression coefficient for e_0 , after adjusting for additional covariates. *GNP* refers to Gross National Product, *MMR* refers to Maternal Mortality Rate, Gini index measures income inequality from 0 (equal) to 1 (unequal).

gross national product, an index of mean schooling attainment, maternal mortality rate, and Gini index of income inequality reduces the effect of e_0 on *TFR* by 76% (Table B2.1.1). Making these kinds of adjustments, however, can be tricky, as most measures of “condition” are imprecise or incomplete (e.g., wealth, socioeconomic status, weight). Thus, in this type of large-scale comparative analysis, even when there is evidence of a trade-off after including multiple controls, we can never be sure we have not missed other confounders, or that the causal arrow is in the right direction.

Trade-offs may be difficult to uncover under conditions of relative abundance, instead requiring studies during periods of resource stress or shortage. Formal modeling of trade-offs, with prior estimates of effect sizes may help researchers to determine sample sizes and other sample characteristics needed to find a trade-off if there is one. The use of natural experiments, longitudinal within-person designs, and instrumental variables may also help to improve causal inference. When possible, trade-offs can also be evaluated by testing for negative genetic correlations among single nucleotide polymorphisms (SNPs) or alleles affecting heritable traits under different environmental conditions, and by using an “animal model” quantitative genetics approach on multigenerational demographic data with pedigrees (e.g., Moorad and Walling 2017).

to certain assumptions. However, Abrams (1993) showed higher extrinsic mortality need not always lead to faster senescence; details about population dynamics and density dependence matter. For example, if population dynamics are density-independent, natural selection does not lead to any relationship between extrinsic mortality and senescence rate (Caswell 2007). The familiar positive relationship occurs when density dependence of higher extrinsic mortality acts primarily on fertility (see also Baldini 2015b).

In Section 2.3, I summarize LHT approaches to the evolved human life history before moving on to exploring within-species variation.

2.3 Models of Human Life History Evolution

Hunter-gatherers with traditional diets and activity regimes, and minimal exposure to modern amenities are an important lens for understanding how selection helped shape the evolution of the human life course (see Box 2.2). Given that quality demographic data with reasonably accurate age and mortality estimation exist only

Box 2.2 | Aché Life History

The Aché of Paraguay were full-time tropical forest hunter-gatherers until the 1970s. After settling in semipermanent reservations, foraging became supplemented by horticulture and increasing access to market goods (Figure B2.2.1). The extensive two-decade demographic study by anthropologists Kim Hill and Magdalena Hurtado provides a comprehensive overview of hunter-gatherer life history blended with rich ethnographic descriptions of childhood, puberty, marriage, and other important life events (Hill and Hurtado 1996). Life history theory is used as a guiding theoretical framework to study mortality, fertility, sexual maturation and growth, and effects of resource availability and kin on these vital rates.

During the precontact period, the major cause of death was conspecific violence due to infanticide and Paraguayan colonists. Accidents and other environmental hazards such as snakebite were also important. Precontact fertility was higher than among !Kung and other hunter-gatherers, at eight live births per woman during a pioneering period with possible changes in forest resource availability. Secondary fatherhood among younger men is presented as an example of a partible paternity strategy, whereby secondary fathers help to contribute resources and lower offspring mortality. Decreasing mortality and high fertility have helped the Aché population recover

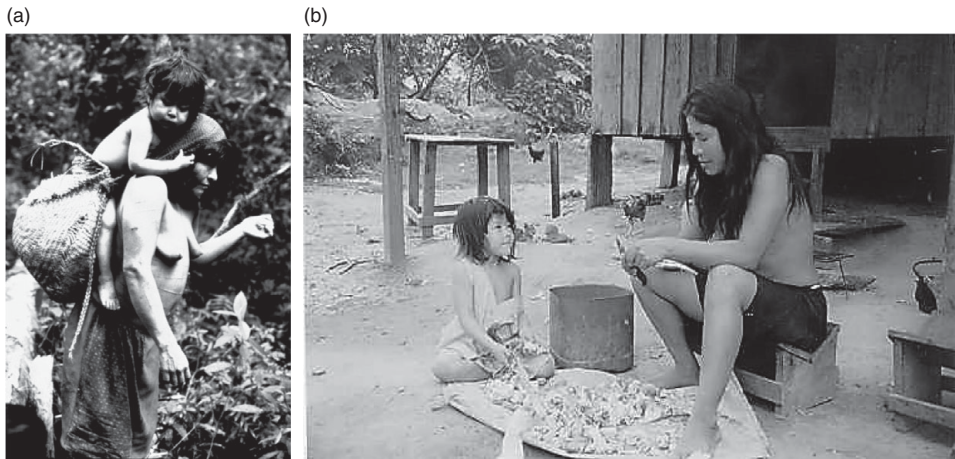


Figure B2.2.1 The Aché of Paraguay. (a) Woman carries her toddler during a forest trek (Photo: Kim Hill). (b) Woman peels sweet manioc root with assistance from her young daughter, at the Arroyo Bandera reservation (Photo: Michael Gurven).

post-contact. Greater resource access is more associated with higher fertility than survivorship, and more so among men and during the post-contact reservation period when Aché were also involved in horticulture.

The timing of first birth and adult body size are predicted remarkably well by modeling the fitness benefits of extended growth and larger body size, using the life history framework developed by Charnov (1993). This framework explicitly models the trade-off between having a higher fertility rate from attaining a bigger body size by growing longer, and having a shorter reproductive window from both delaying reproduction and a lower likelihood of reaching that window. The simple but elegant model not only predicts Aché women's age at first birth but also among !Kung women, and men's larger body size. The latter is because Aché body size has greater effects on male than female fertility, and men can reap these larger gains over a longer reproductive span.

Two curious findings are that early reproduction was associated with higher adult fertility, and that highest fertility is evident among those with the shortest interbirth intervals (~15 months), far lower than the modal 30 months. These results suggest little cost of reproduction, although Hill and Hurtado recognize the difficulty of studying trade-offs in observational studies due to "phenotypic correlations" (see Box 2.1).

Their theoretical and empirical approach raised many new questions, which helped in part, inspire new research directions, among Hadza, Agta and Aka foragers, Tsimane and Shuar horticulturalists, and a new examination of !Kung foragers using a similar life history framework (Howell 2010).

for a handful of populations, horticulturalists provide an additional source of data on mortality and senescence in preindustrial societies. In these populations, up to one-third of individuals are likely to live to age 50, with an expected 15–20 years remaining. With an average age of first reproduction of ~18 years, up to 40% of hunter-gatherer women could expect to reach the age at which a first grandchild would be born (36 years) (Pennington 2001). For hunter-gatherers who survive to the age of reproduction, the average modal adult life span is about seven decades (see Box 2.3). Paleontological evidence is crude, but suggests that a postreproductive life span existed anywhere from 150,000 to 1,600,000 years ago (Bogin and Smith 1996; Caspari and Lee 2004).

Postreproductive life spans are not unique to humans (Cohen 2004; Ellis et al. 2018), having been observed in some cetaceans, elephants, and insects (Figure 2.4). Adaptive explanations should therefore suggest quantitative rather than qualitative differences between humans and other species. Yet most cases in nonhumans and non-cetaceans reflect conditions of captivity or breeding programs that accelerate reproductive senescence, or else the magnitude of postreproductive life is small (Croft et al. 2015).

Several theories have been proposed to explain the extension of the human life span. The classic theory of senescence in evolutionary biology was first proposed by Medawar (1952), developed further by Williams (1957) and then formalized by

Box 2.3 The Seven Decade Human Life Span

The effective end of the human life span under traditional conditions seems to be about seven decades. Following the lead of Kannisto (2001) and Lexis (1878), comparing modal ages of adult death and the variance around these modes provides insight into the stability in adult life spans among populations. The modal age at death may reflect an important stage in physiological decline. By this age, most people experience sufficient decline that if they do not die from one cause, they are soon to die from another. This is consistent with anecdotal impressions of frailty and work effort among aged foragers. While many individuals remain healthy and vigorous workers through their sixties, few are in good health and capable of significant heavy labor in their seventies, and it is the rare individual who survives to their eighties.

Figure B2.3.1 shows the frequency distribution, $f(x)$, of deaths at age x , conditional upon surviving to age 15, for hunter-gatherers and horticulturalists. Data from eighteenth-century Sweden and modern United States are shown for comparison. These premodern populations show an average modal adult life span of about 72 years of age (range: 68–78). There is more variability in the ages of adult death within each of these populations than typically

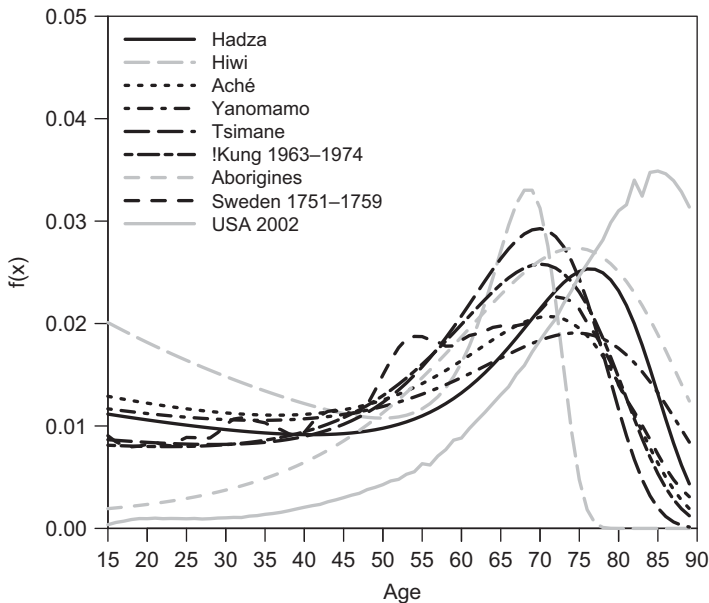


Figure B2.3.1 Modal ages of adult death. Subsistence-level populations of hunter-gatherers, horticulturalists, and eighteenth-century European agrarian farmers show peak ages of adult death ranging from 65 to 80 years. Industrialized nations such as the United States show modal ages of adult death over a decade older than among subsistence populations. Mortality is smoothed using a Siler model for all populations, except Sweden and United States, as described in Gurven and Kaplan (2007).

found in modern industrial populations, due in part to higher age-independent mortality that may be considered different from the “normal” course of aging. The modes are therefore less peaked, accounting for less than 3% of adult deaths. More acculturated hunter-gatherers show the greatest density of deaths after age 55, possibly indicating that as some causes of death (such as violence) are reduced, age-related causes of death become more important leading to a greater density of death around the mode.

Human life span (whether measured as maximal life span, life expectancy, or modal age at death) is longer than predicted for a typical mammal (or primate) of human body size, but not atypical given the larger-than-expected brain size of humans (Allman et al. 1993). Estimates based on regressions of various primate subfamilies and extant apes suggest a major increase in longevity between *Homo habilis* (52–56 years) to *Homo erectus* (60–63 years) occurring 1.7–2 million years ago, and further increases in *Homo sapiens* (66–72 years) (Judge and Carey 2000). Extrapolations for early *H. sapiens* based on comparative analyses, including both brain weights and body sizes among nonhuman primates, similarly suggest a maximum life span between 66 and 78 years (Hammer and Foley 1996).

Although maximum life spans are larger than life expectancies (whose average is often lowered due to high infant and child mortality), it is usually reported that Paleolithic humans had life expectancies of only 15–20 years. This brief life span is believed to have persisted over thousands of generations (Cutler 1975; Weiss 1981) until less than 10,000 years ago when early agriculture presumably caused a slight increase to about 25 years. Gage (2003) compiles over 12 reconstructed prehistoric life tables with similar life expectancies to form a composite life table with survivorship to age 50 (l_{50}) of about 2–9% and e_{45} values of about 3–7 years. There is a large paleodemographic literature concerning problematic age estimation in skeletal samples, and bias in bone preservation leading to underrepresentation of older individuals, calling these previous analyses into question (see O’Connell et al. (1999) and Kennedy (2003)).

Hamilton (1966). It proposes that as individuals age, they contribute less to biological fitness because less of their expected lifetime fertility remains. Consequently, natural selection acts relatively weakly to reduce mortality at older ages. The existence of substantial postreproductive life among humans therefore suggests that older individuals have “reproductive value” by increasing fitness through nonreproductive means (see Box 2.4).

2.3.1 Grandmother Hypothesis

Williams (1957) was first to suggest that beginning at ages 45–50, mothers may benefit more from investing their energy and resources in existing children instead

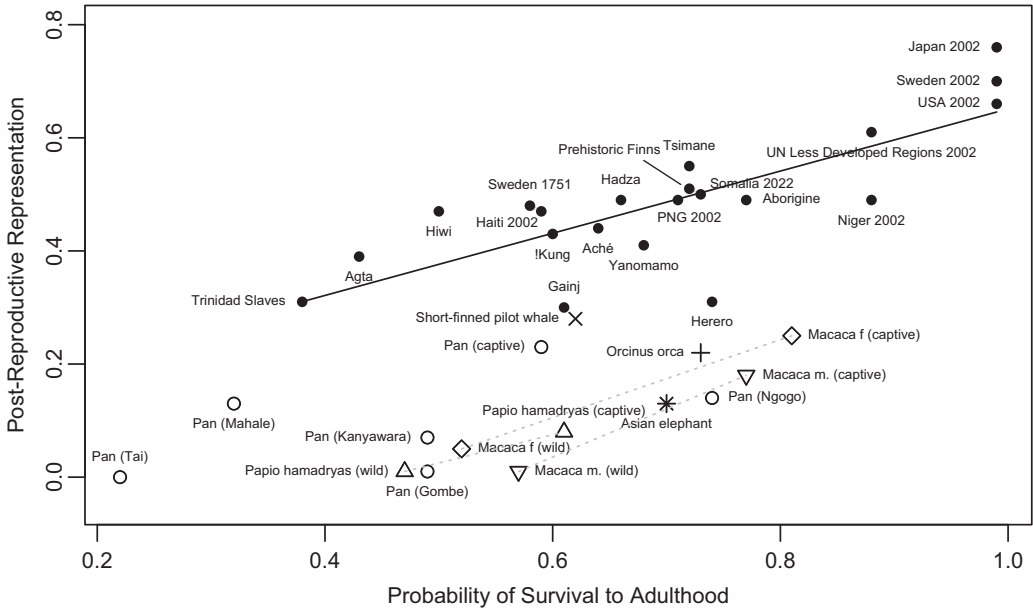


Figure 2.4 Postreproductive life span among humans and other species. I use a standardized measure of postreproductive life span called Postreproductive Representation (PrR), calculated as $l_m/l_b * e_m/e_b$, where l_m is survivorship to post-fertile period (m), e_m is remaining expected life span at age m (see Levitis et al. 2013). Age b is the age at onset of reproduction in adulthood. By considering the proportion of adult years spent in a postreproductive state, PrR incorporates adult survival to age at menopause, and not just years remaining after menopause. Human populations are depicted with darkened circles. Chimpanzees are represented with open circles. Other species with observed postreproductive life spans include killer whales (*Orcinus orca*), short-finned pilot whales (*Globicephala macrorhynchus*) and Asian elephants (*Elephas maximus*).

of producing new ones – that is, the “Grandmother Hypothesis.” Decades later, Kristen Hawkes and colleagues revived this hypothesis (Hawkes 2003; Hawkes et al. 1998), proposing that older women can increase their inclusive fitness by enhancing offspring fertility and survivorship of weaned grandchildren through provisioning younger generations. This version of the proposal was inspired by ethnographic observations among Hadza foragers in Tanzania, where hardworking older women produce substantial quantities of food (see Chapter 6). Among foragers, the resources acquired by women are strength-intensive, disadvantaging young children and thereby increasing the value of older women’s labor contributions. According to this view, extensions of the human life span are driven by selection on women, and the value of resource transfers from grandmothers to grandchildren. This verbal proposal has recently been supported by deterministic and probabilistic models (Kim et al. 2012, 2014) that assume no reproduction after age 45.

Box 2.4 | Why Menopause?

Menopause is viewed as a conundrum when followed by continued survival. How could selection lead to costly investment in maintaining a soma that can no longer reproduce? Extreme altriciality in human offspring, combined with maternal risks of older age births, has been posed as one reason for early reproductive cessation. Chromosomal abnormalities and spontaneous abortions may also be more common at late reproductive ages (Rice 2018). Initial attempts to model the evolution of menopause failed to show that the selective benefits of helping descendants could be sufficient enough to favor fertility cessation over extending reproduction to later ages (Rogers 1993; Hill and Hurtado 1991). Another approach suggests that menopause could be favored when there are resource conflicts among women and their daughters-in-law; asymmetries in kinship, where women would be unrelated to their mothers-in-law's future offspring, but mothers-in-law are related to their grandchildren, gives daughters-in-law the upper hand, and presumably priority reproduction (Cant and Johnstone 2008). This "intergenerational conflict" model, however, has fairly rigid assumptions (e.g., female dispersal and male philopatry, no coercion or synergies in production or childcare, ignores positive kin relationships), and mixed empirical support (Lahdenperä et al. 2012; Mace and Alvergne 2012; Snopkowski et al. 2014).

Chimpanzees rarely survive their reproductive years (Goodall 1986; Jones et al. 2007), and the rate of decline in ovarian follicular stock may even be faster in humans than chimpanzees (Cloutier et al. 2015). Menopause is not likely to be a typical characteristic of chimpanzee life history (Emery Thompson et al. 2007), though among captives at least, negative pregnancy outcomes such as stillbirths and spontaneous abortions do rise with age and parity (Roof et al. 2005). But given the roughly similar age-related fertility declines in humans and chimpanzees (Emery Thompson et al. 2007), human postreproductive longevity has been viewed as the derived trait from a common ancestor in need of explanation. However, why reproductive life span has not tracked increases in life span has not been resolved. It is possible that extension of the female reproductive life span is constrained due to trade-offs associated with the mammalian pattern of restricted oocyte production, where the complete, fixed supply of follicles is established in the second trimester of fetal development, and later subject to processes of gamete selection and decay (atresia) that seems oriented toward preserving embryo quality (Ellison 2001). Improvements in female nutrition and condition have expanded reproductive life span more via lowering the age of menarche than increasing the age of menopause, though secular increases in menopausal age have been reported (Dratva et al. 2009).

2.3.2 Mother Hypothesis

Peccei (2001) amends this view by pointing out that long-term juvenile dependence among humans means that adults will not finish parenting until they are 60 or older if reproduction ceases in their forties. The notion that most of the benefits to longevity derive from helping offspring rather than grandchildren has been called the *Mother Hypothesis*. By no longer reproducing, older mothers can avoid mortality risks of themselves and their offspring from late-life pregnancy. Modeling shows that in the absence of menopause, these risks must rise very steeply with maternal age in order to favor reproductive cessation (Pavard et al. 2008).

2.3.3 Patriarch Hypothesis

Marlowe (2000a) argues that the extension of the life span is driven by selection on men, stressing the fact that men do not experience menopause and can have children into the seventh and eighth decades of life. His argument, called the *Patriarch Hypothesis*, is that as men age they accrue status and power that they use to obtain reproductive benefits. These benefits and the lack of a physiological menopause selects for their greater longevity. Formal demographic models of life history evolution typically focus only on females, but two-sex demographic models where men tend to be older than their spouses may also lead to a pattern of delayed senescence after the age of 50 (Tuljapurkar et al. 2007). In the two-sex model, selection can favor survivorship for as long as men reproduce, lending additional support for the Patriarch Hypothesis. This model, however, requires extensive late-age male fertility more characteristic of polygynous pastoralists (e.g., Gambia) than observed in most hunter-gatherers, and/or mating patterns where fertile women mate with older men, as reported among several Australian and Tasmanian aborigine groups (Rose 1968).

2.3.4 Embodied Capital Model

The *Embodied Capital Model* (ECM) suggests that timing of life events is best understood as an investment process in “embodied capital” – that is, brain-based capital that includes skill, knowledge, and physical abilities that increase fitness (Kaplan et al. 2000; Kaplan and Robson 2002; Gurven et al. 2006). High levels of knowledge and skill are required to exploit the suite of high-quality, difficult-to-acquire resources human foragers consume (Walker et al. 2002; Gurven et al. 2006). Those abilities require a large brain and extended learning phase during a slow period of development, whereby low productivity is compensated for by higher productivity later in adulthood. Gains in adult productivity due to prior investments in skill acquisition therefore select for lowered mortality rates and greater longevity. Thus, ECM proposes that the long human life span coevolved with the lengthening of the juvenile period, increased brain capacities for information processing and storage, and intergenerational resource flows. The related *Reserve Capacity* hypothesis proposes that a supportive social system allowed mothers to wean their children earlier

and to delay maturity, which allowed for a longer period of somatic investment. The larger reserve capacity resulting from a longer parental investment could result in prolonged longevity (Bogin 2009; Larke and Crews 2006).

2.3.5 Control-of-Fire Hypothesis

Though not directly a model of postreproductive life span, the control-of-fire hypothesis complements these models by arguing that human use of fire for cooking helps to increase the efficiency of provisioning by promoting food digestibility and energy, and by allowing early weaning through increased availability of weaning foods (Wrangham 2009). It also further reduces extrinsic mortality by detoxifying certain foods, helping to eliminate food-borne pathogens, and deter predators. However, it should be noted that cooking (especially animal-derived foods) can generate advanced glycation end products, known to increase cancer and diabetes risk due to oxidative stress and inflammation (Prasad et al. 2014).

2.3.6 Other Hypotheses

A model that does not require kin assistance by older adults proposes that post-reproductive life span can evolve as insurance against “life span indeterminacy,” whereby greater variance in somatic and/or reproductive life spans selects for longer postreproductive life spans (Tully and Lambert 2011). The logic is that longer post-reproductive life span reduces the risk of dying by chance before the cessation of reproduction. This idea does not address why females cease to reproduce, nor is it clear for which species it is most applicable. To date, it has only been applied to the arthropod *Folsomia candida*.

2.3.7 Synthesis and Empirical Evaluation?

Many of these evolutionary models and hypotheses are not mutually exclusive. They differ in their focus on women (grandmother, mothering), men (Patriarch), or both sexes (ECM, Lifespan Indeterminacy). The extent to which fitness advantages leading to longer life in one sex leads to coupled longevity in the other sex is sometimes assumed, but need not be the case. For example, female life span exceeds male life span among anthropoid primates where females do the majority of parental care (Allman et al. 1998).

The models also differ in their reliance on resource transfers as primary (grandmother/mother/ECM) or secondary (Patriarch) to life span extension, and whether slow development early in life and life span extension are coupled with economic surplus mid-life and the skills-intensive nature of the human foraging niche requiring learning and instruction (embodied capital vs. grandmother/mother).

All models except the Patriarch and Lifespan Indeterminacy Hypotheses posit that future remaining (caloric) productivity, or productive value (PV_x), can impact fitness even when reproductive value (RV_x) is low or zero. Reproductive value (RV_x) refers to

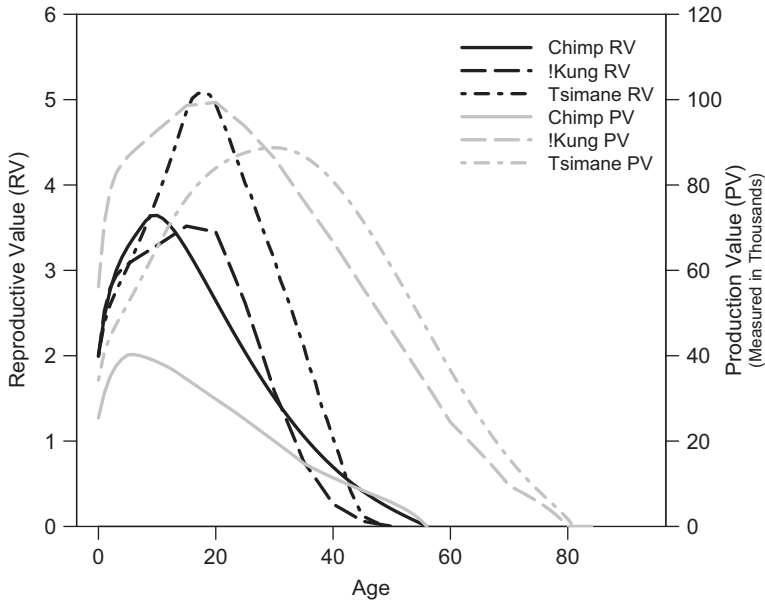


Figure 2.5 Reproductive (RV) and production value (PV) among wild chimpanzees, !Kung hunter-gatherers and Tsimane horticulturalists.

the expected remaining future reproduction for an individual age x . It is calculated from age profiles of fertility (m_x) and survivorship (l_x) as $\frac{e^{rx}}{l_x} \sum_x^\infty e^{-rx} l_x m_x$, where r is the population growth rate and x is age. Among Tsimane horticulturalists, PV_x was estimated as the sum of all future caloric production discounted by future mortality (Gurven et al. 2012). I calculate a similar production value for !Kung hunter-gatherers using age profiles of fertility, mortality, and production in Howell (1979, 2010). When comparing RV_x across humans and chimpanzees, it is clear that they show roughly similar profiles across the life course (Figure 2.5). Humans, however, show a huge surplus of caloric production in midlife, with declines occurring well beyond the reproductive years in both males and females.

Given the ubiquity of food transfers among humans within and across generations, particularly to close kin (see Chapter 6), the high production value in late adulthood can greatly increase fitness impacts of older adults. The fitness impacts of surplus food transferred to kin have been considered vital in the Grandmother Hypothesis and ECM, and other theoretical models invoking resource transfers (Lee 2003b). Aside from food contributions, older adults make “transfers” of aid, advice, instruction, mediation, and other nonfood contributions that can also have important fitness consequences for kin (see Box 2.5). A synthesis of 45 studies shows that relatives other than the mother have protective effects on child survival (Sear and Mace 2008). Aid from grandparents, especially maternal grandmothers, often have positive effects on child survival (see Chapter 13). Though kin effects on fitness extend beyond child survival (e.g., Scelza 2010), the high fitness sensitivities of child survival (Jones 2009) make it the obvious target for kin in high mortality settings.

Box 2.5 | Resource Transfers and Life History in Social Animals

Traditional LHT requires that personal energy budgets cover the costs of growth, maintenance, and reproduction, such that body size and resource production are often highly significant predictors of the pace and timing of fundamental life processes (Stearns 1992). Social animals, however, can lend and borrow critical resources in ways that inflate budgets and allow investments that otherwise would not be possible given exclusive reliance on one's own efforts. The ability to transfer resources, and provide and solicit aid within and across generations can impact selection on age-schedules of mortality and fertility, and prolong life span (Amdam and Page 2005; Lee 2003; Kaplan et al. 2000; Robson and Kaplan 2003). Resource transfers improve the likelihood that juveniles reach adulthood and reduce adult mortality, thereby extending adult life span. Fitness impacts of transfers made by donors of different ages determine the value of being alive at those ages in ways that differ from the standard Hamiltonian formulation of the "force of selection" that includes direct reproduction but ignores transfers (Baudisch 2005; Davison and Gurven 2022). Transfers are often costly to the donor and therefore require that the donor recoups the loss by receiving fitness benefits through shared relatedness, future cooperative exchange, or direct reproduction.

In theoretical models, transfers are not specifically defined, reflecting instead energy flow, production, and fitness enhancement in a content-free way. In order to develop these models further, empirical data are needed on material and nonmaterial transfers in human populations living under similar conditions in which our ancestors evolved. Extant populations of hunter-gatherers and horticulturalists are energy-limited and physically active, experience natural fertility, and lack access to public sanitation, health care, and other modern services that increase welfare. Information on the kinds and frequency of risks afflicting humans in such an environment, and the extent to which transfers help overcome harmful consequences of these risks, is critical for understanding how the human life history evolved.

To date, most empirical work on transfers has focused on food exchange. The human foraging niche allows the possibility of greater risk of food shortfalls over the life course, but also includes other important risks that can impact fitness (Gurven et al. 2012). Illness left untreated can lead to cascading morbidity and possibly death, and often impairs the ability to produce food or perform other important daily tasks. Death or divorce renders dependent children vulnerable to food shortage, disease, and lack of protection, and adults vulnerable to labor shortage. Conflict left unresolved, especially among kin, can result in fractured social and sharing networks, migration, fighting, and homicide. Theft and breakage of important tools, possessions, or other resources can potentially disrupt production and often requires substantial costs to replace. Human cooperation and sociality likely

evolved to reduce risk in these fitness-relevant domains. While instances of nonfood transfers in social species are not rare (e.g., Galef 2001; Carey and Gruenfelder 1997), humans may be unique in the breadth and volume of transfers across different domains. Material and land transfers become especially important for cultural and reproductive success in agricultural populations (Borgerhoff Mulder et al. 2009).

In light of the ECM, it is noteworthy that increases in mortality rates in late adulthood coincide with the rapid declines in PV_x , with lower numbers of potential recipients who are dependent kin (Gurven and Kaplan 2007), and reduced volume of resource transfers (Gurven and Kaplan 2008).

These models were developed to explain the extended life span in the hominin lineage, relative to chimpanzees and other primates, and while mathematical models demonstrate plausibility conditions, there have been no decisive empirical studies that test competing predictions among all of these models. One problem is that conditions maintaining older age today may differ from those that selected for it in the first place. For example, one recent test employing quantitative genetics analyses among a historical sample of Utah Mormons found little support for Grandmother, Mother, or Patriarch Hypotheses (Moorad and Walling 2017). More tests across populations and environmental and cultural contexts are needed to assess the general applicability of these models.

A potential test of generalizability (and parsimony) is if certain models help explain variability in life history traits beyond humans. Killer whales (*Orcinus orca*) have prominent postreproductive life spans (Figure 2.4). Consistent with the mother and grandmother hypotheses, postreproductive females lead their offspring (and sometimes grandchildren or younger siblings) in collective foraging bouts, especially during periods of low salmon abundance (Brent et al. 2015). However, females tend to lead sons more than daughters, given the greater inclusive fitness gains from son investment in their ecology.

Components of the ECM have also found some support in a comparative context. Mammals with greater feeding niche complexity have a later age of adult-level skill competence close to age at first reproduction, subsidized in part by postweaning provisioning, whereas cooperative hunting species (e.g., gray wolves, bottlenose dolphins, spotted hyenas) with greater resource sharing show foraging skill competence peak after age of first reproduction (Schuppli et al. 2012). Slow development in primates and provisioning in social carnivores help to buffer low productivity during learning periods in these species with complex feeding niches (on both dimensions of knowledge and motor-learning), whereas humans employ both strategies. A complex foraging niche is also associated with having a large brain in primates (Schuppli et al. 2016). And across 478 mammals, the source of alloparental care makes a difference for LH outcomes: Greater male care was correlated with the evolution of larger brains, while greater alloparental help was linked to higher fertility (Heldstab et al. 2019). Finally,

a metabolically explicit mathematical model of brain life history evolution consistent with the logic of ECM successfully predicts human brain and body mass, foraging skill development throughout ontogeny, and humanlike childhood and adolescent life stages (González-Forero et al. 2017).

It is worth noting that none of the models addresses more recent changes in the human life span, nor specify proximate mechanisms by which life span is extended. Since the early 1800s, human life expectancy has increased worldwide, due to rapid declines in infant and child mortality; however, late-age mortality has continued to decline as well, and the modal age of adult death has also increased by at least a decade (Vaupel 1997). Caleb Finch and colleagues have argued that genetic changes responding to alterations in infectious exposure, nutrition, and inflammatory immune responses over the course of hominin evolution are responsible for the lengthier life spans of humans, and the ability for improved environmental conditions to continue lowering mortality rates (Finch 2012). A gradual reliance on scavenging, hunting, and cooking could have altered the selective environment among hominins relative to forest-dwelling apes. Greater meat and fat consumption, and pathogen exposure from scavenged meat, and noninfectious inflammagens (including the advanced glycation end products that speed up oxidative damage to cells, implicated in the etiology of many degenerative diseases) from cooked food would have selected for “meat-adaptive” genes. One of the more important of these includes apolipoprotein E alleles that are pro-inflammatory to heighten immune responses. While advantageous in high-infection contexts like in ancestral populations, pro-inflammatory genotypes unique to humans have had adverse consequences in the low-infection environments of the past century on cardiovascular disease and brain aging (Finch and Sapolsky 1999; Finch and Stanford 2004). These genetic changes might explain why captive chimpanzees do not experience the same degenerative diseases as in industrialized populations of humans (Varki et al. 2009).

2.4 Within-Species Human Variation

2.4.1 Human Life History: Slow vs. Fast Pace?

Life history theory’s tools (i.e., trade-offs, optimization, and constraints) have been employed to help explain within-species variability among humans, including differences among subgroups, and even individuals within a population. Species tend to vary along a slow-fast life history continuum as a function of mortality risks and predictability (Roff 1993). The existence of a slow-fast continuum in LH strategies is an inductive generalization based on comparative data, rather than a derivation of formal LHT. Yet, similar logic and testing finds that individuals in the same species may vary in life history pace as well, though the extent to which individual-level LH strategies can be summarized along one dimension is debatable (see Section 2.5.1, Box 13.1). Nonetheless, the logic of LHT has had wide-reaching expanse in the social and psychological sciences (see Section 2.4.4). In a classic study, Margo Wilson and

Martin Daly showed that life expectancy across Chicago neighborhoods varied by as much as 23 years, even after removing effects of homicide; they proposed that such salient differences shape reproductive timing and risky behavior (Wilson and Daly 1997). Expanding upon this view, people who perceive themselves living under harsh conditions that are difficult to control are more likely to abstain from healthy habits, including routine physical activity, a healthy diet, physician checkups and preventative care, not because of poor understanding of the health consequences of such abstention but because other uses of time and money may take precedence if chronic disease risks at later ages are discounted (Nettle 2010b; Pepper and Nettle 2014). Cigarette smoking, alcohol consumption, drug use, criminal behavior, overeating, risk-taking, and other activities that provide short-term gains but long-term costs have all been associated with (perceptions of) living in an unpredictable, high-mortality environment (Adams and Nettle 2009; Arndt et al. 2013; Bickel et al. 1999; Nettle et al. 2017). Medical treatment compliance, adherence to a healthy diet, safer sexual practices, regular physical exercise, and other activities that may provide long-term benefits but have immediate costs are similarly associated with an unpredictable, high-mortality environment (Christensen et al. 1991; Huston and Finke 2003; Kosteas 2015; Wardle and Steptoe 2003).

Faster life histories where future prospects look dim may also shift priorities toward earlier and greater reproductive effort, including earlier sexual maturity, sexual activity and reproduction, greater short-term mating, and higher total fertility (Chisholm et al. 1993; Ellis 2004; Gur et al. 2019). These relationships comprise part of the cost of reproduction. Rapid reproduction, multiple dependency, and relatively high fertility of humans – greater than expected for a primate of our size – are hallmark features of the evolved human life history. Prior to widespread transitions to low fertility around much of the world, human natural fertility was characterized by repeated pregnancies, intensive breastfeeding, and multiple concurrent dependent offspring. At what cost to survival is this heavy investment in reproduction? *Disposable soma* theory suggests that investments in maintenance will improve longevity but at the cost of reproduction (Kirkwood 1990), hence no organisms are immortal. Conflicts are thus expected between investing in somatic maintenance versus reproduction under energetic constraints. When exogenous mortality is high, greater and earlier investments in reproduction are expected, resulting in an accumulation of damage, faster senescence, and lower postreproductive survival (Kirkwood and Rose 1991; Kirkwood 2002).

I address this central idea regarding how trade-offs between different life history investments can affect survival from three complementary levels of analysis: demographic, physiological, and psychological.

2.4.2 Demographic Applications

While several studies provide support for an inverse relationship between fertility and longevity in humans (e.g., Doblhammer and Oeppen 2003), others show no, or even a positive, relationship between completed fertility and human life span

(Gavrilova et al. 2004; Helle et al. 2005). However, most of these studies rely on historical demographic data, focus on mortality, and often are unable to control for differences in reproductive timing, maternal energy budgets, and selection effects (Hurt et al. 2006; Gagnon 2015). One study using the same methods and selection criteria across three historical datasets over several centuries (Utah, two provinces in Quebec) showed similar negative effects of parity on postreproductive survival (Gagnon et al. 2009). They also showed a consistent positive effect of age at last birth, but no effect of age at first birth on postreproductive survival.

Even if total reproduction is not consistently associated with life span as predicted by the disposable soma hypothesis (see Box 2.1), the timing and intensity of reproduction can still generate costs that affect different aspects of maternal health and fitness. A separate literature on “maternal depletion syndrome” examines trade-offs between fertility and health by studying both the short-term and cumulative long-term impacts of repeated pregnancies in developing countries. The additional nutritional and metabolic costs of pregnancy and lactation (Butte and King 2005), combined with immune modulation and increased susceptibility to certain infections during pregnancy (Jasienska 2009) can place a substantial burden on maternal health and nutritional status, at least in the short term. For example, pregnancy in well-nourished women with gestational weight gain of 12 kg is estimated to cost an additional ~70 kcal/day in the first trimester to ~440 kcal/day in the third trimester (Butte and King 2005). Lactation is even more costly, increasing metabolic rate by ~25%, protein needs by up to 54% and vitamin/mineral needs up to 93% (Dewey 2004). Given these costs, it may be surprising that evidence for sustained maternal depletion due to repeated, closely spaced reproductive bouts is mixed (Tracer 2002). However, most studies are cross-sectional and rely on one or two anthropometric measures to assess overall nutritional status while overlooking other aspects of somatic condition. The problem of phenotypic correlation is particularly relevant here (see Box 2.1); women in better condition and with greater resource availability may experience higher and faster fertility, and better health outcomes (Stearns 1992; Hill and Hurtado 1996).

One recent example among living women in a natural fertility population is revealing. Tsimane women of the Bolivian Amazon have nine births over their lifetime. Despite high fertility in an energy-limited, high pathogen burden environmental context, higher parity and faster reproduction were not robustly associated with longitudinal deficits in women’s nutritional status or with biomarkers of nutrition or immune activation (Gurven et al. 2016a). Postreproductive women continue to gain weight, body fat, and BMI with age, irrespective of the short-term deficits they experience during their reproductive years.

2.4.3 Physiological Applications

The study of proximate physiological mechanisms can help to illuminate trade-offs suggested by LHT (see Chapter 14). For example, endocrine regulation of several LH trade-offs related to parenting versus mating effort, and current reproduction versus

immune function have helped to clarify important functional aspects (Ketterson and Nolan Jr 1992), and future studies focusing also on hormone receptors and hormone regulation of gene expression will be instructive (see Chapter 14 for examples). Whereas costs of reproductive effort have been studied largely in terms of maternal and postreproductive mortality, studies of living organisms permit opportunities to examine effects on physical state. Insights into lowered somatic maintenance due to more intense reproductive effort can be gained by exploring relationships between reproduction-related variables and biomarkers of “aging” that gauge phenotypic condition. One set of such biomarkers assesses “oxidative stress.” Physiological costs increasing energy metabolism (e.g., pregnancy, lactation) generate free radicals and damaging reactive oxygen as a consequence of mitochondrial functioning and the electron transport chain. When such metabolic damage is not sufficiently repaired, this can lead to oxidative stress. Oxidative stress has thus been proposed as central to somatic decline and aging. Two biomarkers related to such stress include 8-OHdG (biomarker of DNA oxidative damage) and Cu-Zn SOD (antioxidant defense enzyme). Among women living in southern Poland engaging in heavy seasonal farm labor, the number of lifetime pregnancies was associated with both higher 8-OHdG and Cu-Zn SOD (Ziomkiewicz et al. 2016). Despite this interesting result, whether oxidative stress causally links reproductive effort and somatic decline remains controversial (Speakman and Garratt 2014).

High calcium demand and altered estrogen concentrations during pregnancy and lactation may also deplete bone mass, resulting in lower bone mineral density (BMD), especially in high-fertility populations with intensive breastfeeding. Low BMD can indicate osteopenia or osteoporosis, and increase fracture risk. Lower BMD in the spine and parts of the femur were observed in postmenopausal Turkish women of high parity compared to low parity controls (Gur et al. 2003). Among Tsimane women, early first birth, high parity, and short interbirth intervals were associated with lower BMD levels in the calcaneus (Stieglitz et al. 2015). But BMD relationships with parity are less consistent in western populations characterized by low fertility, higher energy budget, and positive weight gain over successive pregnancies. Greater reproductive investment by women has also been linked to tooth loss, captured in multiple languages by the phrase “a child, a tooth” (Christensen et al. 1998), though several plausible mechanisms may explain the relationship.

While affluent environments may enable greater investment in both reproduction and survival, comparison of the hormonal milieu among populations can provide insight into the effects of energy budget on trade-offs (e.g., Ellison et al. 2002; Nuñez-de La Mora et al. 2007). Women and men in affluent countries tend to have higher reproductive hormone concentrations than those in poorer countries and among traditional populations with natural fertility. Yet, the costs of cumulative hormonal exposure may affect health at later ages. High estrogens have been associated with hormone receptor-positive breast tumors (Boddy et al. 2015), and high testosterone with greater prostate cancer risk (Alvarado 2013). In high-income countries, higher parity is sometimes associated with weight gain, and greater risk of obesity, diabetes, and cardiovascular disease (see Chapter 14 for further details).

Immune defense as a principal form of somatic maintenance has multiple components reflecting additional life history trade-offs (Figure 2.3). Innate, or nonspecific, immunity develops at low initial cost, but can be mobilized quickly to fight novel pathogens, albeit at high operating costs. Acquired, or specific, immunity is costly to develop, mobilizes against known pathogens more slowly but at relatively low cost. McDade et al. (2016) provide a framework that considers how different environmental factors might shape investments into these two areas of immune function. They propose that nutritional abundance, high pathogen exposure, and lower exogenous mortality should favor a greater emphasis on acquired immunity, whereas resource scarcity, low pathogen exposure, and high exogenous mortality should favor greater investments in innate immunity. Preliminary applications of this framework in the Philippines suggest these environmental influences early in life may shape the character of immune expression in adulthood (Georgiev et al. 2016).

Trade-offs among immune subcomponents are especially salient during a woman's reproductive years. It has been proposed that insuring fetal tolerance during pregnancy requires immunologic changes that might compromise a mother's defenses against certain infections (e.g., reducing inflammation, increasing regulatory T cells and innate immune activity). For example, pregnancy increases risk of pneumococcal pneumonia, influenza, and malaria, and also increases the severity of these and other infections (see Kourtis et al. 2014 for review). Likewise, some bacterial and viral infections inducing inflammatory immune responses can impair fertility outcomes. For example, bacterial vaginosis increases risk of first trimester miscarriages (Ralph et al. 1999). Cytomegalovirus, influenza, dengue, and other preventable infections account for up to 15% of early miscarriages (<12 weeks) and up to 66% of late miscarriages (12–24 weeks).

2.4.4 Psychological Applications

Much research in the social sciences addresses effects of the *amount* of social and economic resources on health and life history-related traits. However, the *predictability* (i.e., stability) of resource access on life history-related decision-making is less appreciated. Living in harsh, unpredictable environments characterized by resource insecurity, ecological uncertainty, volatile safety nets, and unsafe neighborhoods can foster a present-oriented disposition that favors short-term benefits despite long-term costs, while discounting long-term benefits that carry short-term costs (Pepper and Nettle 2014; Hill 1993). Consistent with this notion, young adults living in slums (*favelas*) of Rio de Janeiro were found to discount the future more heavily than age-matched Brazilian university students (Ramos et al. 2013). Across 46 nations, those with greater life expectancy (proxy for better conditions) were more willing to wait for a larger but delayed reward (i.e., less present-oriented) (Bulley and Pepper 2017). To date, the few experiments testing effects of harshness on time preference reveal similar findings as in observational and comparative studies. For example, inducing cues of poverty among Chinese students revealed more impulsivity and present-oriented preferences (Liu et al. 2012).

Though less explored, a growing number of studies have started to link proxies of a faster life history trajectory to psychological traits other than time preference. Dispositional traits proposed to have been shaped by living under resource-insecure conditions include higher impulsivity, less self-regulation, low self-efficacy, and an externalized locus of control – that is, believing that one’s own efforts may have only marginal effects on well-being. Thus, in terms of motivation to improve one’s health, a relatively stable environment with predictable resources and low extrinsic mortality risk should favor greater self-efficacy and a more internalized health locus of control orientation due to the payoffs from successful planning. Such planning requires a sense of control and an ability to self-regulate in ways that help realize delayed gains at short-term cost, especially in the presence of numerous stressors.

Consistent with this line of reasoning, experimental evidence reveals that low levels of control lead to a lower ability to focus on concrete goals (Keltner et al. 2003), a belief that goals are not attainable (Anderson and Galinsky 2006), less motivation to realize goals (Galinsky et al. 2003), and greater future discounting (Joshi and Fast 2013). Across 43 nations using World Values Survey, lower income within and among countries was associated with lower perceived control, intrinsic motivation, and trust (Haushofer and Fehr 2014). Among seven postcommunist countries, the effects of socioeconomic status and material deprivation on health were mediated largely by perceived control (Bobak et al. 2000). Thus, resource limitation, harsh environment, and uncertainty about the future may lead to undervaluing long-term health. Further support is evident in a recent study of Tsimane Amerindians, who exhibit less internal and more external locus of control than representative, age-matched samples from the United Kingdom and Japan; Tsimane with external locus orientation are less likely to seek medical attention for common illnesses (Alami et al. 2018).

Living in poverty with many stressors and low sense of power is also believed to induce greater “cognitive load,” leading to cognitive biases and poor decision-making (Sheehy-Skeffington and Haushofer 2014). But in contrast to the standard “deficit” approach where adverse environments are believed to result only in impairments and underachievement, invoking an adaptive flexibility framework posits that being raised in adverse or high-stress conditions develops traits that are better suited to managing these conditions. A growing body of evidence suggests selective enhanced abilities among vulnerable and at-risk populations, and more so when stressful conditions are artificially induced in the laboratory. These enhanced abilities include greater attention shifting, memory for negative events, rapid visual tracking of threats, recognition of angry and fearful faces, enhanced learning about animal dangers, enhanced early life memory retention, and empathic accuracy (see Ellis et al. 2017 for review).

These examples extend the logic of LHT to help explain individual differences in psychology and behavior. It is tempting to think that these and other traits can vary systematically along a slow-fast LH continuum. The more successful and promising approaches explore relationships between (early) environment and one or two limited LH domains (see Section 2.4.1).

2.5 Unresolved Issues and Future Directions

The following sections selectively highlight six areas that could benefit from further study.

2.5.1 Pace of Life, Psychometrics and LHT

The life history prediction relating extrinsic mortality to life pace-related traits is derived from a cross-species framework. However, many applications of LHT in humans reflect differences across individuals within a population, sometimes modeled as facultative adjustments made during the course of development (e.g., Frankenhuis and Panchanathan 2011). While inferences at the individual level carry the logic of LHT, they are not necessarily derived from it, nor do they carry the nuance of the original models (see Section 2.1.1). Indeed, analysis of the LHT literature shows that recent studies are more about fast–slow “pace of life” (especially in humans) than formal, model-driven LHT (Nettle and Frankenhuis 2019).

As partly showcased in Section 2.4.1, current LHT studies in the social and psychological sciences often reflect generalized “slow” versus “fast” life history strategies. Despite growing enthusiasm, caution and further theory development are warranted (see also Box 13.1). First, the generalizability of the extrinsic mortality–life history pace relationship has not been widely explored across conditions, such as during periods of population decline, nor across cultures, subgroups, by sex, class, or other contexts. Even the widely cited relationship between father absence and early pubertal onset may be more complex than typically portrayed in earlier treatments based on western urban populations (Sear et al. 2019).

Second, the extent to which human individual life history pace can be generalized along a single dimension is controversial and, in many cases, not theoretically derived from LHT. Though Eric Charnov helped inspire current understanding of the slow–fast continuum across mammals (Charnov 1993), and across primates (Charnov and Berrigan 1993), his formal analysis focused on a few key demographic traits with clear links to biological fitness. However, common psychometric batteries aimed at assessing slow–fast life history strategies (e.g., High-K Strategy Scale, Mini-K, Arizona Life History Battery) combine some obvious LH-related traits like time preference, risky and self-maintenance behaviors, with many others, such as competitiveness, mating behavior, cooperativeness, personality traits, social attitudes, parenting styles, and affect. Aside from the methodological difficulties of measuring these using (often) self-administered questionnaires, many of these are conceptually distant from more traditional life history traits, may not be functionally coordinated, and carry dubious or contradictory links to fitness. Perhaps unsurprisingly, confirmatory factor analyses show that these aggregate bundles reflect multiple, often orthogonal domains – not a unidimensional indicator of overall life history pace (Copping et al. 2014; Richardson et al. 2017).

Another problem is that by combining many facets, high-order psychometric factors tend to conflate proximate mechanisms with ultimate-level functional

explanation, resulting in incorrect inferences (Gruijters and Fleuren 2018). Instead of representing a latent global LH strategy with theoretical coherence and predictive validity, these instruments instead generate descriptions of correlated phenomena rather than causal explanations (Richardson et al. 2017); they describe lifestyle rather than evolved LH strategies. More attention to formal LHT is needed here, as well as proximate mechanisms, relating measures and constructs to fitness-related outcomes in a more coherent, hypothesis-driven manner.

2.5.2 Perceptions and LHT

As highlighted in Sections 2.4.4 and 2.5.1, psychological studies have the potential to assess cues related to key inputs affecting life histories. Even when individuals experience similar traumas or inhabit similar environments, *perceptions* of events and *attitudes* concerning future prospects can vary in key ways that affect decision-making. Starting with some influential theorizing by Draper and Harpending in the early 1980s on the role of early environment on adult reproductive behavior (Draper and Harpending 1982), it is commonplace to believe that psychological traits are shaped by exposures early in life (Chorpita and Barlow 1998; Gale et al. 2008; Lynch et al. 1997), even though sometimes they can change with circumstances over the life course (Rodin 1986; Schneider et al. 2006). Understanding how perceptions are first formed, the timing of experience in shaping those perceptions, and how new information updates them, are all interesting questions of obvious life history relevance. The question of perception formation and updating is especially relevant in the context of rapid cultural, socioeconomic, and political change. Different personalities may also perceive and react differently to similar exposures. Personality differences may themselves reflect evolved life history differences (Biro and Stamps 2008; Wolf et al. 2007).

The approach highlighted in Section 2.4.4 relating life history pace, time preference, and psychological traits presents a promising direction for further exploration of population differences in psychological and behavioral traits. With improved health infrastructure and other forms of socioeconomic development occurring globally but at different rates, perceptions of uncertainty, and environmental harshness should shift accordingly, with concomitant impacts on psychological traits affecting behavior. Yet, even in high-income countries, natural disasters and other unexpected traumatic events can, at least temporarily, shift perceptions in the opposite direction. For example, exposure to Hurricane Katrina was associated with altered risk preferences (Eckel et al. 2009). In low-income countries, floods and other disasters can lower aspirations, and affect risk and time preferences in ways that might contribute to poverty traps (Kosec and Mo 2017).

2.5.3 Cooperation and Conflict in the Extended Human Family

The label “cooperative breeding” applied to female reproduction refers to all of the help from non-mothers, including fathers, siblings, grandparents, and other kin and nonkin (see Chapter 12). While aid can help lower female work effort, shorten

interbirth intervals, and improve offspring survival and growth, assuming joint interests and complete cooperation within extended families is an oversimplification. Unlike other cooperative breeding systems, human systems contain multiple breeders, and so domains of conflict of interest are to be expected. To date, there has been little systematic study of how extended household economic decision-making occurs. For example, how is it determined who is to accomplish different tasks on a daily basis? To what extent are tasks coordinated to maximize household or group production? Given the large networks of potential allocaretakers and recipients available, how are competing interests navigated? Theoretical and empirical work exploring these dynamics and their implications on resource transfers and cooperative breeding are needed in future studies of human sociality.

2.5.4 Population Dynamics in the Past vs. Ethnographic Present

Most contemporary hunter-gatherers and small-scale horticulturalists experience positive population growth, on average ~ 1%. Such growth could not have represented conditions over long stretches of our species history: In order to achieve population stationarity (i.e., zero growth), mean fertility would have to be well below that ever observed in natural fertility populations (to a total fertility rate of 4 births per woman) or survivorship would need to be lower than ever observed (Gurven and Kaplan 2007). It does not appear that ethnographically studied hunter-gatherers inhabit more marginal environments than neighboring farmers (Porter and Marlowe 2007; Cunningham et al. 2019). So either conditions during ethnographic study are not representative of the past (e.g., warfare may have been more common), or population dynamics over time may be better characterized by periods of growth followed by rapid population crashes (i.e., a “saw-tooth” pattern) (Hill and Hurtado 1996). It is difficult to evaluate these two possibilities in light of current knowledge about the past, but a recent study suggests a combination of altered vital rates and population crashes were common throughout human history (Gurven and Davison 2019). While evidence suggests that climate varied widely throughout the Pleistocene and into the Holocene epoch (Richerson et al. 2005), the extent to which past foragers typically experienced increasing, declining, or zero growth in past environments is unknown, yet better indirect evidence is necessary (e.g., Fernández-López de Pablo et al. 2019). A long evolutionary history of booms and busts could suggest different selection pressures than those under stationary population dynamics. For example, evolved risk and time preferences, sensitivity to plasticity, and decision-making impacting fertility, health, and conservation behavior may differ under constant versus variable selection regimes.

2.5.5 The Role of Cumulative Culture

The multigenerational structure of resource transfer is a foundation supporting human life histories (see Box 2.5; Chapters 5 and 12). While resource flows have been considered in a multigenerational framework (e.g., Hooper et al. 2015b), the role

of social learning and information transfer in impacting production and other fitness-relevant behavior has not been formally integrated into life history models, nor measured empirically (see Chapter 15). Tolerant social relations promoting partial connectivity with out-groups can help foster the spread and development of complex cultural traits (Derex and Boyd 2016). Maintaining long-distance connections with nonkin is not uncommon among hunter-gatherers, facilitated in part through ritual and affinal relationships (Hill et al. 2014). How this social structure and tolerance of ingroup and outgroup strangers evolved requires attention. Also, the importance of (costly) information transfer to help improve skill development early in life and adult productivity, especially in the context of a difficult foraging niche, has not been formally modeled. Aside from instruction, other “non-productive” roles of older adults, such as storytellers, musicians, shamans, ritual specialists and as “walking libraries” have yet to be modeled formally nor has their functional significance been widely tested (Sugiyama 2011; Schniter et al. 2018; Smith et al. 2017; cf. Gurven et al. 2020).

2.5.6 Expanding beyond Foragers and Students

Given the task of explaining the evolved human life history, much attention to date has been with populations believed to be most representative of our ancestral past – that is, hunter-gatherers and small-scale horticulturalists, or convenient samples of university undergraduates. While farmers and pastoralists have been studied, there are no comparable life history studies as comprehensive from birth-to-death as say, the Aché, !Kung, Hadza, or Tsimane. This may be due in part to the relative dearth of long-term ethnographic and demographic studies of small-scale populations (see Chapter 17). Fertility transitions and the uptake of family planning have complicated the study of reproductive behavior, whereas subsidized health care, public health infrastructure, and lowered cost of food have affected other aspects of life histories. Though cumulative material wealth, schooling, health insurance, and other novel socioeconomic conditions present theoretical and empirical challenges, their consideration offers exciting choice domains to consider when modeling adaptability and optimal decision-making (Gurven 2018). The focus on proximate currencies like status or wealth, and their link to fitness under some conditions but not others, is a recurrent theme in studies of urban populations (e.g., Kaplan et al. 1995a; Shenk 2004; Goodman et al. 2012). Current focus of studies on development and nutrition, human capital investments and fertility decline, wealth inheritance, and kin cooperation in urban populations could benefit from greater integration with other life history-related themes, including life span, mortality risks, aging, and immune function. Indeed, long-term multigenerational studies still reveal a signature of selection on LH traits even in contemporary low-fertility populations (Stearns et al. 2010).

2.6 Conclusion

Life history theory has been successfully applied across the biological sciences to explain how socioecological context affects how organisms should differentially

allocate limited resources to navigate a wide range of decisions shaping survival and reproduction. Life history theory is a productive framework for determining optimal trait characteristics given trade-offs defined by costs and benefits of different possible “solutions” to fitness-relevant problems. In this chapter, I first introduced and evaluated competing accounts of the human adaptive complex of life history traits that evolved from that of a more chimpanzee-like ancestral precursor. I then summarized how LHT informs our understanding about human variability in demographic traits such as fertility, mortality, life span, physiological traits such as immune defenses and bone mineral density, and psychological traits such as time preference and impulsivity. Finally, I pointed to unresolved issues and future directions for new generations of scholars to improve our understanding of both intraspecies life history variation among humans, and human-typical life history traits in comparative context. Life history theory as a discipline is just over half a century old, and it branched from ecology to the human life sciences only over the past several decades. Indeed, much of the exciting work cited in this chapter is recent and a promising sign of growing interdisciplinary efforts, extending LHT from demographic traits to new areas of sociality, psychology, energy acquisition, and health.