

Fertility Theory: Theory of Life History Evolution

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Abstract

Variation in fertility patterns in relation to environmental factors and mortality schedules can be understood using evolutionary life history theory. In addition to explaining differences within and between human populations, LHT allows us to make direct comparisons with other species. Here we discuss LHT, the concept of trade-offs, and the importance of this theory as applied to humans. We end by discussing the ways in which LHT potentially explains patterns of low fertility in contemporary industrialized society.

“Life histories lie at the heart of biology; no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles.” Stearns (1992, p. 9)

In 2014, the world population topped 7 billion, with almost all observed population growth occurring in the less developed world. At the same time, evidence suggests that global fertility rates are actually beginning to decline, with almost all developing nations showing some sign of entering a demographic transition (e.g., Sanderson 2013). In the industrialized world, where fertility has been in decline for over a century, total fertility rates hit an all-time low in the 1990s, dipping below replacement levels. Yet, recent fertility projections suggest this pattern may now be reversing, with fertility set to rise to replacement levels, and perhaps beyond, raising the intriguing possibility that reproductive strategies may be shifting in response to the conditions of the post-industrial world (Myrskylä et al. 2009, 2013). What determines the number of children a woman will produce in her lifetime? How can we make sense of the fertility patterns we see, and understand why they vary in both time and space?

These questions have long engaged demographers, economists and sociologists, but fully satisfactory answers continue to elude us. These are also questions that, in broad perspective, evolutionary biologists seek to answer about all species, as they relate directly to measurements of fitness (approximated by the number of descendants that contribute to future generations), and hence to the action of natural selection, the process by which adaptive evolutionary change occurs. Our goal here is to show how aspects of evolutionary thinking can be brought to bear on questions relating to human fertility patterns, and that, although we are not yet able to solve all the puzzles of human fertility variation, we can begin to address these issues in ways that productively augment more traditional social science approaches.

Life history theory and the cost of reproduction

Life history theory provides a robust evolutionary framework in which to situate studies of human reproductive and mortality schedules, in ways that also allow us to make direct comparisons with other species. An organism’s life history is the combination of the probabilities of survival and fecundity that a species displays in its natural environment (Partridge & Harvey 1988); it is therefore closely tied to the study of demography (Stearns 1992). The theory of life history evolution posits that fitness is maximized by natural selection over the lifespan of an animal. This is not as easy as simply maximizing fertility¹ at every age, as fertility in early life may be traded-off for decreases in either fecundity, fertility, or survival in later life. That is, there is a cost to reproduction.

Why is reproduction costly? One reason is that there are ecological costs associated with the act of reproducing. For most (if not all) animals, the environment is a dangerous place: acquiring resources, mating, giving birth and raising young are all activities that leave animals prone to physical injuries, exposed to disease or at risk of death by predation (Roff 1992). More importantly, reproduction is costly because it requires

¹ By fertility we mean the total number of offspring produced, whereas fecundity refers to the potential to reproduce.

energy that must be diverted away from other bodily processes (the “Principle of Allocation”). An animal’s life history is a consequence of three biological processes that compete for resources in the body: repair (or maintenance), growth, and reproduction. Investment in reproduction inevitably decreases the amount of energy that can be invested in repair and growth and, as a consequence, decreases future fecundity and survival. These trade-offs - the costs paid in terms of fitness when a beneficial change in one trait is linked to a detrimental change in another (Stearns 1992) - are a fundamental concept in LHT.

The cost of reproduction, and its associated trade-offs, not only affects an individual’s own fecundity and future survival, but also that of its offspring. In an elegant study, Dijkstra et al. (1990) manipulated brood size (i.e., the number of chicks produced in a single breeding attempt) in kestrels, a small bird of prey, either adding or removing two nestlings to some nests (as well as leaving some nests untouched). They found that adding nestlings increased the total number of fledglings produced, but that the offspring in such nests had the slowest growth and highest nest mortality rates compared to nests that were reduced in size. Moreover, when raising an enlarged brood, male parents spent much more time in flight and flight-hunting, whereas female parents were lighter, and lost weight more rapidly. Most strikingly perhaps, the parents of enlarged broods also displayed lower survival. The cost of reproduction, therefore, is multifaceted, with both intra-generational effects (decreased survival of the parents) and intergenerational effects (reduced offspring survival, decreased mass of offspring).

Life histories are characterized by these kinds of trade-offs that, in one way or another, serve to balance the energetic resources allocated to current versus future survival and reproduction. The form such trade-offs take, and hence the life-history trajectory followed, depends critically on the nature and quality of the environment an organism encounters because this will differentially influence the chances of survival and reproduction.

How large and how soon?

Many organisms must first reach a minimum size before they are able to reproduce, simply because a certain level of bodily development is needed to support any kind of reproductive function. Growth is often extended beyond this minimum body size, however, because a larger body size is beneficial for fecundity and juvenile survival. All else being equal, then, animals try to maximize body size. The amount of time an organism spends growing to achieve larger body size hinges directly on environmental conditions. Better quality environments lead to increased growth and hence larger, more fecund adult animals. In poor environments, growth is slowed due to reduced energy intake, which may lead to reduced adult size, but large body size may also be less favorable under such conditions, as this incurs greater costs of maintenance and repair. For a number of species, including humans, growth ceases entirely once reproduction begins (so-called “determinate” growth), and selection pressures and trade-offs change dramatically once this point is reached; hence the switch from the growth phase to the reproductive phase (i.e., the age of sexual maturity) is a particularly crucial transition in an animal’s life history.

Sexual maturity is usually defined as age at first birth in LHT, rather than by any physiological measure of maturation (Stearns 1992). The benefit of maturing at an early age is largely self-evident: it reduces the chances of dying before an individual has had the chance to reproduce. Furthermore, offspring of early-maturing animals will themselves mature earlier relative to the offspring of later-maturing animals and hence start reproducing sooner. Delaying maturity when mortality risk is low can also be advantageous, however, because extended growth and larger size may increase the chances of survival, as well as initial and future fecundity, the number of reproductive events, and the quality of the offspring or parental care provided.

Environment-specific mortality risks thus strongly influence age at sexual maturity. Higher mortality reduces life expectancy, such that animals cannot 'afford' to postpone reproducing, and hence will mature at an early age, trading this off against a longer growth period and larger adult body size. Conversely, low mortality in later life results in later maturation, allowing individuals to reach a larger adult size. The relationship between low mortality and delayed age at first birth has consistently been documented, across species, across populations within species, and within populations. For instance, among humans, cross-national average age at first birth shows a strong negative association with mortality rates in those countries. Even at quite small scales, such as within a city, mortality predicts the timing of first birth (Nettle 2011). Although Nettle (2011) did not consider the relationship between mortality and growth as the source of these differences, other studies have shown an interaction between patterns of growth, mortality and age at maturity across populations (Walker et al. 2006).

How varying environments lead to reaction norms

As the above makes clear, the trade-off between age and size at maturity, which in essence represents the trade-off between current and future reproduction, is environment-specific. If a species occupies an environment that is either very stable over time, or the species' range is very narrow, natural selection will likely have solved the optimality problem such that all animals will mature at a specific body size X and age Y (although, of course, there may be some genetic variation between individuals that gives rise to phenotypic or trait variation). Now imagine that a species occupies a broader range of environments and is likely to face more variable environmental conditions as a result. This variation produces variation in growth rates and age- and size-specific mortality rates (Stearns & Koella 1986). Under poor environmental circumstances, for example, growth will be slowed substantially. If the animal still matured at body size X under such conditions, it would take considerable time to reach this point; this would be risky given that mortality may strike before the animal reaches this size. If, however, the animal matured at an earlier age, Y , it would do so at a very small adult size, which would also impose a cost in terms of future survival and fecundity. A different compromise between X and Y is therefore needed to reach an optimal outcome for this specific environment. When the environments that animals encounter are variable in this way, "reaction norms" are likely to evolve. A reaction norm is a set of phenotypes produced by a single genotype across a range of environmental conditions, and allows animals to track the optimal trade-off. Thus, phenotypic variation across environments may represent the

expression of an evolved reaction norm, which ensures an appropriate trade-off between life history components. It is also true that some of this variation can arise from genetic variation across individuals in the reaction norms themselves.

The finding that rates of mortality across neighborhoods within a city predict age at first birth potentially can be interpreted as an expressed reaction norm (Nettle 2011), because these phenotypic differences are unlikely to be (solely) due to genetic differences. Cross-populations differences in age at first birth and patterns of mortality also fit well with LHT predictions: as the chance of reaching adulthood decreases, earlier onset of sexual maturity is generally observed (Walker et al. 2006). These patterns cannot, however, be unambiguously interpreted in terms of a reaction norm. In some pygmy groups, for instance, sexual maturity occurs early and at very short adult stature in environments of high mortality, and these characteristics are linked to distinct hormonal profiles with a genetic basis, suggesting the action of natural selection on early reproduction, rather than a plastic response to the environment. Indeed, testing for reaction norms remains an ongoing challenge as we still know surprisingly little about population-level patterns and individual-level biological processes in relation to age, growth rates and size at maturity (Walker et al. 2006; Stearns 1992).

How many and how much to invest?

The next decision an animal faces once it has reached the reproductive phase is how many offspring it should produce, and how many resources it should invest in them. Any energy invested in the current offspring entails costs in terms of future survival and offspring production (Dijkstra et al. 1990). Although in many species, clutch (or litter) size can be adjusted, the same does not hold for all animals, including humans. Humans are generally restricted to a litter size of one, as are most other primates. Current theorizing suggests that producing a low number of offspring on a regular basis is adaptive in primates, because of their long lifespan and their reliance on a highly variable resource base, both of which leave them vulnerable to unpredictable shortfalls in available resources -- and hence to low juvenile survival -- during any particular breeding attempt (Jones 2011). By limiting their reproductive effort to a single offspring at a time, mothers are able to invest more in their own survival, thereby increasing their lifespan and ensuring a larger number of reproductive events. In this way, reproductive failure in any one year is not catastrophic in terms of fitness (Jones 2011).

There is, however, a rather unusual case in humans, which sheds light on the cost of reproduction, namely twinning - a relatively rare event (0.6–4.5%; Lummaa 2007). Compared to women who have singleton births, mothers of twins have a higher risk of dying during childbirth, longer subsequent birth intervals, are more likely to terminate reproduction entirely, are more likely to fail to raise their next offspring, and are more likely to die earlier in the post-reproductive phase (Lummaa 2007). Moreover, twins are usually smaller in size than singleton births and experience lower survivorship (Sear et al. 2001). Mothers who give birth to twins are also larger in size than those who give birth to singletons (Sear et al. 2001), suggesting that twinning is indeed costly and that larger maternal body size is needed to bear these increased costs. The cost of twinning extends to both the parents (intra-generational) and the offspring themselves (intergenerational).

Twinning, however, may also provide advantages in terms of fitness, if the costs of reproduction are offset by the benefits of gaining two offspring from a single birth event (Sear et al. 2001). For example, Lummaa et al. (1998) observed that lifetime reproductive success of mothers of twins was higher in areas of high resource availability, but lower in areas of low resource availability compared to mothers of singletons. Moreover, they showed that rates of twinning were higher in those areas in which twins provided fitness advantages, providing some support to the notion that natural selection may maintain, or even favor, twinning under some circumstances (Lummaa et al. 1998).

Although humans generally produce only one offspring per reproductive event, they are rather unusual in that, due to a long period of offspring dependence, parents usually raise several offspring of varying ages simultaneously, with resources distributed over all children raised. Indeed, humans are different from other primates in a number of respects: in addition to a lengthy developmental period and dependence on caregivers, we also possess large expensive brains, have a relatively long adult life, and display intergenerational systems of resource flow. All these traits have been argued to stem from the fact that humans are adapted to a particularly skill-intensive foraging niche, in which many years of learning are needed to reach high levels of competence (Kaplan et al. 2002). Attempting to raise a series of children whose demands on parental care overlap in time inevitably leads to conflicts, given that resources are finite. As children are both heavily dependent and energetically costly in their first years of life, the biggest conflicts often arise when births are very closely spaced in time. Indeed, there is substantial evidence that shorter interbirth intervals increase child mortality (Hobcraft et al. 1983; Koenig et al. 1990). The negative effects of twinning on survival as discussed above - a case in which the lowest possible interbirth interval is achieved - also fit well with these patterns.

The adverse effects of short interbirth intervals are generally considered to be a consequence of either 'maternal depletion syndrome' (i.e., mothers do not have sufficient time to recover from the physiological and nutritional demands associated with pregnancy, parturition, and breastfeeding) or the competition between siblings over parental resources (Koenig et al. 1990). These effects are arguably strong enough to have led to the evolution of lactational amenorrhea: a postnatal period of infecundity that arises as a consequence of hormonal changes induced by breastfeeding (Howie & McNeilly 1982). Indeed, breastfeeding is the most widely used method of controlling birth spacing in populations without modern contraception; the energetic demands of milk production are high, and nursing offspring represents a significant constraint on the availability of metabolic energy to support a new pregnancy (Ellison 2003). As LHT predicts, then, investment in current offspring strongly limits females' ability to invest in future offspring.

Fertility, longevity and the difficulties of measuring life history trade-offs

In principle, identifying trade-offs between different life history trade-offs should be straightforward, given an understanding of underlying theory and a species' ecology. In practice, however, it is not so easy. A consideration of the trade-off between fertility and

survival illustrates this point perfectly. For species that reproduce repeatedly, like humans and other primates, this trade-off is dependent on both the spacing of births, and on the total number of dependent young that need to be raised to adulthood. Increasing resources in reproduction detracts resources from both parental investment into children (which should reduce their quality and hence their chances of survival), and also from bodily maintenance (which should lead to reduced parental survival). Studies of the trade-offs between fertility, child survival and parental survival, however, reveal anything but consistent results (Lawson et al. 2012; Gagnon et al. 2009), with both positive as well as negative relationships observed.

Although there may, of course, be plausible theoretical reasons why fertility can potentially increase child or parental survival (for example, under some conditions, children may be successful at procuring resources for themselves and the family, changing the dynamic of the trade-offs in such ecologies: Lawson et al. 2012), the variability seen may also reflect the difficulty of accurately measuring trade-offs. Obviously, experimental methods (such as manipulating clutch size or breeding experiments; Roff 1992) are not possible in humans, and we are left with either assessing phenotypic correlations between life history traits or genetic correlations between traits based on family data. These correlational methods necessarily set boundaries on the confidence we can place on the results obtained. For example, unidentified confounding variables may give rise to relationships that are counter to life history predictions (it should be noted, however, that this problem is most definitely not restricted to humans; Partridge & Harvey 1988; Stearns 1992). One such confound is the quality of the individual, or more specifically, the energy budget the individual has at its disposal. To put this in everyday terms, one might predict that most people would be able to afford either an iPad or an iPhone, given the expense of such items, and so would have either one or the other, but not both (i.e., there would be a trade-off). For individuals with a larger bank balance, however, such compromises are unnecessary; they can afford to buy both an iPad and an iPhone. The presence of such differences across individuals in the resources available can easily obscure the true nature of the trade-offs operating (Noordwijk & Jong 1986). Another complicating factor is that our ability to identify trade-offs may be clouded by the presence of genotype by environment interactions, such that different genotypes respond differently to different environments (see Stearns (1992) for further discussion). These underlying difficulties may account for variation in, or lack of, observed trade-offs in a population.

Even when a predicted trade-off is observed, we often cannot infer causality because of the correlational methods used. For instance, increased reproductive effort (i.e., higher fertility) should come at a cost of parental effort (i.e., levels of parental investment), and indeed recent studies show that high fertility is often negatively related to child survival (Lawson et al. 2012). It is also possible, however, that the causality here is reversed: when mortality is high, women may increase their fertility in an effort to 'replace' deceased children, and/or they may pre-emptively increase fertility because they expect to experience a certain level of child mortality (Lawson et al. 2012; Winterhalder & Leslie 2002). Although research on humans is unlikely to completely overcome the measurement difficulties identified above, the greater availability of databases containing

LHT-relevant information, and their higher quality in terms of both sample size and level of detail, along with more advanced statistical methods, may well overcome these limitations to some degree (Lawson et al. 2012; Gagnon et al. 2009).

Quantity, quality, and the demographic transition

Among industrialized societies, advances in medical science and public health have reduced child mortality to very low levels. Consequently, any reduction in parental investment may not manifest itself in terms of reduced offspring survival, but may be more nuanced. For example, high fertility is related to many adverse consequences for offspring due to competition between siblings. A larger number of siblings has been found to reduce grades at school, adult education and income, height, and health (Lawson & Mace 2011), providing strong evidence for the trade-off between the quantity and quality of children.

It is exactly this trade-off that has been suggested, in the evolutionary literature, as the main explanation for the demographic transition (the switch from high to low fertility and mortality regimes that accompanies economic development and industrialization). Kaplan's (1996; Kaplan et al.'s 2002) embodied capital theory is worth highlighting in this regard as it explicitly incorporates aspects of prominent economic theories of quantity-quality trade-offs (Becker 1960; Shenk et al. 2013), along with demographic theories of fertility (Bongaarts 1978), into an evolutionary life history model². The theory treats growth, development and maintenance as investments in stocks of embodied capital in both self and offspring. Importantly, this embodied capital includes knowledge and skills, as well as somatic tissue, thus bringing cognitive abilities into the realm of life history theory. For humans, growth of knowledge may be as important as bodily growth with respect to adult competence and ultimately fitness maximization.

Kaplan's (1996; Kaplan et al.'s 2002) starting point is to argue that fertility regulation mechanisms are adapted to the selection pressures of the learning-dependent, skill-intensive hunter-gatherer foraging niche. Natural selection is hypothesized to have acted on human psychology such that people are sensitive to the environmental variation in learning opportunities and their likely pay-offs, and levels of parental investment are calibrated accordingly. Individuals adaptively adjust levels of parental investment via breast-feeding (i.e., via one of the primary proximate determinants of fertility), lactational infecundability, as modelled by Bongaarts (1978), and nutritional flows to women (which also relates to lactational infecundability, both directly by affecting milk production, and indirectly via women's workloads and energy balance). Under conditions where all "wealth" comes in the form of energy from food, the accumulation of embodied capital is automatically translated into offspring, via female reproductive physiology. Kaplan et al. (2002) demonstrate that, when applied to hunter-gatherer life-ways, a model of embodied capital maximizes fitness.

² There are a number of other theories of the demographic transition in the literature (see Shenk et al. (2013) for review), particularly those that focus more heavily on cultural explanations, but we will not discuss these here, as our aim is to illustrate how life history theory attempts to explain this phenomenon in terms of the relevant trade-offs.

Kaplan (1996; Kaplan et al. 2002) then considers contemporary societies, asking what factors would prompt a decline in fertility. One key factor is argued to be the emergence of extra-somatic forms of wealth (livestock, land, money), which breaks the link between parental investment and reproductive physiology. Whereas somatic wealth translates directly into fertility under hunter-gatherer conditions, because our evolved psychological preferences for resources under such conditions amount solely to those energetic resources that can be stored in the body, this same psychology leads us astray when extra-somatic wealth can also be accumulated; this is argued to be because there is no mechanism in place to ensure that this evolutionary novel form of wealth is translated into fertility (Kaplan et al. 2002). Indeed, the model shows that a preference for wealth-maximization under these conditions can lead to maladaptive behavior of the kind identified by Becker (1960), where people favor income and consumer goods over children. It should be noted, however, that this argument rests on the assumption that we possess an evolved psychological mechanism of this nature, and that this has failed to keep pace with the cultural and economic changes that characterize industrial societies. More stringent tests are needed to demonstrate the existence and operation of such a mechanism, and show that it is unable to respond adequately to wealth-accumulating environments.

A second factor linked to declining fertility that Kaplan (1996; Kaplan et al. 2002) identifies relates to the changing pay-offs of embodied capital investments in low-mortality industrial contexts compared to hunter-gatherer lifeways. In essence, low mortality, combined with increased demands for skilled workers, is argued to result in high expected returns from investing heavily in the embodied capital of each child produced (in terms of educating them to the level required to be competitive in such societies). As family wealth is finite, this requires a trade-off between producing a few highly educated, skilled offspring versus a larger number of poorly educated, less skilled, less competitive offspring. Under such conditions, people calculate the number of children they believe they can afford to raise, given their wealth, and regulate their fertility accordingly.

Thus, even though in physiological terms, individuals have the capacity to produce large numbers of children, Kaplan (1996; Kaplan et al. 2002) argues that the high costs of providing them with the kinds of embodied capital needed to compete successfully, combined with the distorting effects of extra-somatic wealth on people's preferences, results in very few children actually being produced. Kaplan et al. (2002) therefore suggests that, although individuals trade-off offspring quality against quantity exactly as predicted by life history theory, in modern environments this number falls below that required to maximize fitness.

Yet, when extra-somatic energy use is considered (i.e., the use of fossil fuels, and the infrastructure required to support these) modern human fertility has decreased relative to other primate species exactly as expected given our increased energy consumption (Burnside et al. 2012). More specifically, human birth rates display an allometric relationship with energy expenditure in line with that of other species, and this pattern is quantitatively consistent with the life history patterns seen in other mammals, as well as

non-industrial human populations. As an example: the energy use of a woman in the US nowadays is equivalent to the metabolic rate of a hypothetical 30.000 kg primate, and fertility rate is similar to what one would expect for a primate of this size (Burnside et al. 2012). Although industrial societies have larger more complex networks that can distribute larger amounts of energy resources than non-industrial societies (pipelines, power grids, railway and road networks), such networks also require longer transport times for such energy to be distributed, and experience greater infrastructure costs. Burnside et al. (2012) therefore argue that, when all the relevant costs of raising children are factored into the equation, it becomes clear that offspring in industrial societies require exceptionally heavy investment, resulting in an extreme trade-off whereby very few children of very high quality are produced. When viewed from this perspective, the issue of whether people are behaving maladaptively and failing to maximize fitness remains open.

Indeed, there are a number of mathematical models demonstrating that small families may maximize fitness. Mace (1998) shows that when inherited resources contribute strongly to fitness, and the cost of raising children is high, very low levels of fertility can be favored. Moreover, reducing fertility may enhance fitness in the far future if ‘snowballing’ effects of wealth are possible such that income generates income (Hill & Reeve 2004), when long-term reproductive outcomes are more predictable (Winterhalder & Leslie 2002) or when population dynamics are taken into account, such as (environmental) calamities resulting in demographic crashes (Boone & Kessler 1999).

The most convincing empirical study to date, however, suggests that lowering fertility may not, in fact, maximize long-term fitness. Using data on over 14000 Swedes born in the early 1900s, Goodman et al. (2012) showed that low fertility increased descendants’ socioeconomic position (in line with the quantity-quality trade-off), but decreased their biological fitness. As the period covered by this study includes many demographic and societal changes that individuals had never encountered before, it remains possible that people’s decision-making was in a state of flux, leading to maladaptive behavior in response to these changeable circumstances. Indeed, people’s ability to track and respond to risk is not perfect (Winterhalder & Leslie 2002). Although highly speculative, it seems possible that, as shifts in mortality schedules and costs of raising children may now have stabilized, people may be able to make more accurate assessments of environmental circumstances, and adjust their fertility in ways that ultimately contribute to higher fitness. Recent forecasts indicating that fertility may again be on the rise in some European nations (Myrskylä et al. 2013), can perhaps be interpreted in just this fashion.

Conclusion

The social sciences have been very successful in identifying the relevant determinants of fertility, both within and between populations (Balbo et al. 2013), but these determinants are often studied in a disjunct fashion. A life history approach posits that reproduction is inextricably linked to other processes in the life cycle of an animal, with ecology determining how energy is allocated to these processes, and it thus argues that all aspects of the life cycle should be studied in tandem. The currency that is optimized in LHT, and more generally evolutionary theory, is the number of surviving offspring (or even the

number of surviving offspring that contribute to the next generation). Incorporating such measures into studies of fertility, in addition to the number of children born per woman, would bring evolutionary and social science approaches closer together. A union of these approaches will augment and enhance our understanding of fertility, while placing humans in their appropriate evolutionary context, allowing us to make direct comparisons with other species.

Cross References

Anthropology - Reproduction, Anthropological Approaches to;
Demography;
Demography - Life Table;
Demography - Demographic Measurement: General Issues and Measures of Fertility;
Demography - Evolutionary Biodemography;
Demography - Fertility Theory: Theory of Intergenerational Wealth Flows;
Demography - Fertility Theory: Embodied-capital Theory of Life History Evolution;
Studies of the Life Course - Human development, Bioecological theory of;
Studies of the Life Course - Plasticity in Human Behavior across the Lifespan;
Studies of the Life Course - Fertility Theory;
Evolutionary Sciences;
Evolutionary Sciences - Adaptation, Fitness and Evolution;
Evolutionary Sciences - Human behavioral ecology;
Evolutionary Sciences - Evolutionary Demography;
Environmental and Ecological Sciences - Ecological Anthropology;
History - Historical Demography
History - Life Course in History
Studies of the Life Course: Lifespan Development: Evolutionary Perspectives

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