

Fertility Transitions

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Abstract

Demographic transitions in contemporary human societies have profound
impacts on our social and economic lives (Dyson, 2010). Across the population
sciences, there are abundant empirical observations, but few causal explanations,
10 of fertility transition. The seeming contradiction between observed fertility
patterns and fitness-maximization assumptions pose a significant challenge
for evolutionary theorists. In this chapter, we explore evolutionary theories
that can potentially help address this deep theoretical challenge. We argue
that cultural evolutionary approaches can tackle aspects of fertility transitions
15 that other approaches neglect. Finally, to bridge divides between evolutionary
and non-evolutionary perspectives, we highlight intersections between cultural
evolutionary theory and other social, economic, and political sciences.

Keywords: demographic transition, fertility decline, human reproduction, cultural evolution

20 1 Demographic Transition: An Overview

Demographic transition refers to the long-term population trends in human societies in which birth rates and death rates fall from high to low values along with “modernization” and economic development (Notestein, 1945; Thompson, 1929; Kirk, 1996). Together with the Industrial Revolution, these two historical phenomena are
25 associated with tremendous economic growth and consequent social and political transformation, shaping the contours of the modern world. The sustained economic and income growth we are used to today was not possible before around the 19th century, when humans are assumed to have been in a “Malthusian trap” or fluctuating equilibrium (Malthus, 1798) under which any extra agricultural production
30 was immediately consumed by the additional growth of population size, leading to “natural checks” on further population growth (though see Boserup, 1975; 1976 for an alternative explanation). New technologies and manufacturing processes brought about by the Industrial Revolution, combined with more saving and investment per capita brought by lower fertility (Coale and Hoover, 1958; Higgins and Williamson, 1997; Oppenheim Mason, 1997; Bloom and Canning, 2001) are argued to now ex-
35 empt us from this trap.

Demographic transitions have immense social and economic implications for our world (Reher, 2011). For example, most of the global population now lives in coun-tries where fertility rates will hardly replace the population. Shrinking, ageing and
40 long-lived populations are expected to significantly increase labor shortages and impact pension systems, decreasing income and economic growth, social mobility, health care quality, and living standards in the future.

While “demographic transition theory” (Thompson, 1929; Notestein, 1945; Kirk, 1996) highlights several stages for this phenomenon, the transition is basically de-
45 termined by two major forces: mortality decline and fertility decline. In the course of economic development and modernization, mortality drops first while fertility remains high, resulting in rapid population growth. Fertility rates then begin to fall, slowing down population growth and changing the age structure, from younger to older (Chesnais, 1990).

50 Mortality decline has received a great deal of attention (see Wilson, 2011) and we have a relatively good grasp of its causes: improvements of farming techniques, food production, and public sanitation contributed massively to the reduction of diseases and the increase of life expectancy. The reasons for fertility decline, on

the other hand, remain complex despite appearing straightforward. At the macro
 55 level, indexes of development like HDI (human development index), are strongly
 and negatively associated with fertility rates (Lee, 2003; Bryant, 2007; Myrskylä
 et al., 2009), both across countries and over time within countries. It is therefore not
 surprising that the constituent measures in the HDI, namely, per capita income (Luci
 and Thévenon, 2011; Myrskylä et al., 2009; Barthold et al., 2012), education level
 60 (Lutz and Kc, 2011; Axinn and Barber, 2001), and life expectancy (Lutz et al., 2006;
 Luy et al., 2019) are all negatively correlated with fertility rates. Other correlates of
 fertility rates include child mortality, religiosity, urbanization and population density
 (Lutz et al., 2006), income inequality (de la Croix and Doepke, 2003), gender equality
 (Myrskylä et al., 2013; Feyrer et al., 2008; McDonald, 2000), and family planning
 65 uptake (Cleland and Wilson, 1987).

At the micro level, individual low fertility is correlated with high male and female
 education, in turn associated with lower mortality, longer life expectancy and higher
 child survival rates, and these effects are stronger in high fertility countries (Lutz
 and Kc, 2011; Basu, 2002). Fertility is also proximately regulated by later ages at
 70 first birth and greater control over reproductive spacing and stoping behavior. In
 many cases, these practices are facilitated by contraceptive use (Cleland, 2009) and
 constrained by some “intermediate” fertility variables such as induced and spon-
 taneous abortion, fecundability (the ability to conceive), and marriage (Bongaarts,
 1982). With greater autonomy granted by changes of either labor participation or
 75 contraception methods, women appear to exercise more “control” over their repro-
 duction and their desired family size decreases as macro-level development proceeds
 (Goldstein et al., 2003; Pritchett, 1994).

But fertility decline is not solely driven by socioeconomic factors, it also diffuses
 like an epidemic (Rogers, 1995b; Rosero-Bixby and Casterline, 1993; Spolaore and
 80 Wacziarg, 2022, see Cleland, 2001 and Colleran, 2016 for review). There is over-
 whelming evidence to suggest that fertility decline is spread by social interactions,
 both between individuals and between neighboring countries and regions. More-
 over, fertility decline is diffused between countries at increasingly lower levels of
 economic development (Bongaarts and Watkins, 1996; Montgomery and Casterline,
 85 1996), with different cultural settings influencing the patterns of diffusion and on-
 set of fertility decline (Knodel and van de Walle, 1979). Thus fertility levels can
 vary greatly between neighbouring areas with similar socioeconomic characteristics
 (Lesthaeghe, 1977, 1983; Alvergne and Lummaa, 2014; Colleran et al., 2014). Indeed,

the patterning of contraceptive uptake cannot be understood without assuming that
 90 new ideas are diffused along established communication lines, by migration and the
 mass media, which can readily cross international borders (Barber and Axinn, 2004;
 Behrman et al., 2002; Watkins, 1991; Cleland and Wilson, 1987). Contraceptive
 uptake is especially linked to micro level social interactions within social networks
 (Montgomery and Casterline, 1996; Rogers and Kincaid, 1981; Mace and Colleran,
 95 2009; Colleran and Mace, 2015; Alvergne et al., 2011; Colleran, 2020). The evident
 connections between sociocultural factors and demographic transition indicate that
 the process could be driven by the diffusion of new ideas and changes in percep-
 tions (Axinn and Yabiku, 2001; Oppenheim Mason, 1997; Cleland and Wilson, 1987;
 Colleran, 2016).

100 Despite ample evidence for the above factors, they are mostly correlational indi-
 cators and few of them can be causally separated from one another. This means that
 what appear to be law-like patterns in fertility change across and within populations
 are associated with everything all at once. Our poor understanding of causality is
 clearer if we look at the temporal relationships of these factors. Although one of
 105 the major efforts by the Princeton European Fertility Project (Coale and Watkins,
 1986) marks the historical fertility decline at around 1830s in France, several other
 studies in economic history consistently found even earlier records of the onset to
 be around 1770s in French rural areas (Spolaore and Wacziarg, 2022; Blanc and
 Wacziarg, 2020; Cummins, 2013; Hadeishi, 2003; Weir, 1995). However, none of
 110 the correlates for fertility decline mentioned above seemed to be operating during
 this earlier period. For example, child mortality is often argued to be the most
 important explanation for fertility transition (e.g. Notestein, 1945). But in histor-
 ical France, it was net fertility (i.e. average number of births minus deaths) that
 was declining (Blanc and Wacziarg, 2020). And in the 19th Century U.S., there
 115 was no meaningful fall of mortality before fertility decline (Haines, 1994; Guinnane,
 2011): this occurred only after 1900s when improved medical science led to greater
 longevity (McKeown, 1976; Fogel, 2004; Deaton, 2006). Overall, our understand-
 ing of the causes of fertility decline remains limited, particularly when we examine
 a multitude of complications at different levels of aggregation and the temporal
 120 relationships of various factors.

2 Evolutionary Perspectives

Fertility transitions are even more puzzling from an evolutionary perspective. Why does a great ape that outcompeted and out-reproduced its competitors, whose population size exploded with the advent of agriculture (the “Neolithic demographic transition”, see Bocquet-Appel, 2011), reduce its fertility exactly when the environmental conditions for reproducing are the best in its entire history? Why does the process begin in the richest, most long-lived strata of society, and why is it more dramatic there (see Clark and Cummins, 2009; Livi-Bacci, 1986)? How can voluntary reductions in fertility be in line with Darwinian fitness (Borgerhoff Mulder, 1998; Colleran, 2016)?

In a 1986 paper, Vining suggested that this conundrum is an evolutionary paradox, the now oft-cited “central theoretical problem of human sociobiology” (Vining, 1986). Though this claim may be somewhat of an overstatement (see invited comments in Vining, 1986; Borgerhoff Mulder, 1998; Alvergne and Lummaa, 2014; Stulp and Barrett, 2016), Vining’s clarion-call sparked debate about the fundamental causes of demographic transitions from an evolutionary perspective (Mace, 2000; Lawson and Mace, 2011; Shenk, 2009; Borgerhoff Mulder, 1998; Colleran, 2016). Standard demography, though empirically rich, has not produced a fundamental and unifying theoretical framework for understanding why fertility declines. Evolutionary researchers should therefore be well-positioned to fill this gap. Yet convergence on a single evolutionary explanation has not occurred, mainly because of differing assumptions about the mechanisms giving rise to low fertility, the question of whether fertility decline is adaptive or not, a tendency for researchers to focus on either socioeconomic or sociocultural factors and on individual versus population-level effects (Colleran, *Forthcoming*).

There are at least three starting points for an evolutionary approach to fertility decline. First, fertility decline could be the result of a mismatch between an evolved psychology and contemporary environments. Evolutionary Psychology (EP) asserts that our psychological biases evolved in ancestral environments over the last two million years, and that evolved strategies for achieving status and sex are therefore not adapted to the radical changes in modern industrialized economies (Cosmides and Tooby, 1987; Tooby and Cosmides, 1990; Buss, 2019). This “adaptive lag” (Laland et al., 2016) leads to low fertility when efficient contraceptives became available (Pérusse, 1993), cutting the link between sex and reproduction. From

155 this perspective, fertility decline is simply a “maladaption”, where our previously-
adaptive psychology has not yet caught up with environmental change, and is not
expected to maximize genetic fitness. This view, however, needs to demonstrate: (1)
why fertility-limiting behavior has not been selected out of the population; (2) why
fertility started to decline in historical Europe even before modern contraceptives
160 emerged (e.g. Spolaore and Wacziarg, 2022; Blanc and Wacziarg, 2020), and (3)
must reconcile the fact that the availability of contraceptives does not necessarily
lead to their uptake (Polgar and Marshall, 1976; Marshall, 1977; Levine, 1983) and
fertility decline (Alvergne et al., 2013; Mace and Colleran, 2009; Bledsoe, 2002).

A second approach views low fertility as an adaptive strategy under contem-
165 porary environments. Taken by many human behavioral ecologists (HBEs), this
approach stresses analysis of the costs and benefits of reproductive behavior in any
context, but also the potential maximization of genetic fitness over multiple genera-
tions. The currencies of fitness being maximized include future gene representation
(i.e. the number of descendants), the “quality” of offspring, or the accumulation of
170 wealth over generations (see more detail in next section).

A third approach views fertility behavior as fundamentally shaped by infor-
mation that is socially acquired, and is therefore the outcome of cultural evolu-
tionary (CE) processes in structured environments. Thus, cultural processes may
follow Darwinian principles, but may nonetheless be maladaptive and not fitness-
175 maximizing. In fact, asymmetric transmission of information, biases in the ways
that individuals acquire social information, structural change in social interactions,
or between-group competition, can all spread norms and values that lead to fitness-
limiting behavior. Since both individual-level mechanisms and group-level dynamics
are jointly considered, this approach offers a multi-level perspective that can engage
180 both individual-level mechanisms and longer-term population dynamics.

Importantly, although most evolutionary research on demographic transition is
concerned with comparing the explanatory weight of hypotheses from HBE and
CE (Lawson and Mace, 2011; Shenk, 2009; Borgerhoff Mulder, 1998), many re-
searchers now agree that socioeconomic and sociocultural factors are too deeply
185 intertwined to be isolated from one other (Oppenheim Mason, 1997; Easterlin and
Crimmins, 1985; Lesthaeghe, 1983; Caldwell, 1976). In fact, these two frameworks
make overlapping assumptions and predictions, as others have pointed out (Shenk,
2009; Borgerhoff Mulder, 1998; Colleran, 2016; Colleran, *Forthcoming*), so they are
not mutually exclusive (Smith, 2000). In many cases, the assumptions of HBE and

190 CE are complementary in explaining demographic transition to low fertility. In the next two sections, we explore these two theoretical frameworks in more detail.

3 Human Behavioral Ecology

Human behavioral ecology (HBE) is concerned with the evolution of human behavior as a response to ecological conditions (Nettle et al., 2013). The area centers
195 on the concept of fitness maximization and adaptation, and attempts to explain behavioral variations among and across human populations. The general questions human behavioral ecologists ask include: how behavior influences an individual's survival, why (in terms of evolutionary function) a particular behavior is present over others, and how the functions and outcomes of behavior are moderated by
200 different environmental contexts.

HBE centers around the assumption that humans adapt to specific ecological contexts to maximize their genetic representation in future generations. According to life-history theory (Kirkwood et al., 1991; Roff, 1992; Stearns, 1992), individuals allocate their limited time and energy budgets into a series of life events —
205 birth, maturation, reproduction, death, etc. This involves fundamental trade-offs. For example, reproducing reduces the energy available to spend on somatic maintenance, puts stress on maternal survival and nutritional condition (Tracer, 1991), or reduces lifespan (Lund et al., 1990; Westendorp and Kirkwood, 1998). Individuals must therefore make cost-benefit decisions when achieving their goals (Stearns, 1989;
210 Lawson and Mace, 2011; Mace, 2000; Volland, 1998; Cronk, 1991; Borgerhoff Mulder, 1992), including parental investments in their own (Williams, 1957; Stearns, 1989) or their children's survival (Hobcraft et al., 1983), when and how often to have children (Blurton Jones, 1986), how many children to have, and how many resources to allocate to each of them (Lawson and Mace, 2011).

215 These fundamental trade-offs are reflected empirically in the facts that (1) humans almost never exhibit maximal biological fertility (Lawson et al., 2012 2012; though see Strassmann and Gillespie, 2002 for an exception), (2) that very high fertility only appears to be sustainable in agricultural societies (Bentley et al., 1993; Bocquet-Appel, 2011) where the costs of reproduction can be partially compensated
220 via food storage and reduced mobility (Bocquet-Appel, 2011), and (3) tight birth intervals (Blurton Jones, 1986) and high fertility (Strassmann and Gillespie, 2002; Lawson et al., 2012; Penn and Smith, 2007; Meij et al., 2009; Gillespie et al., 2008)

are typically negatively associated with offspring survival, even though lowering fertility to improve child survival does not translate into greater lifetime reproductive output of parents (Lawson et al., 2012; Penn and Smith, 2007; Meij et al., 2009; Gillespie et al., 2008; see Strassmann and Gillespie, 2002 as an exception).

3.1 Reproductive Trade-offs

Given these considerations, many researchers, both in the evolutionary and social sciences like economics, view low fertility as a parental investment trade-off between offspring quality and quantity, where every unit decrease in quantity is assumed to lead to an increase in “quality” (Becker, 1960; Becker and Lewis, 1973). While quantity is easily measured, quality can refer to different things in different disciplines or even socio-ecological contexts.

In the evolutionary literature, “quality” usually refers to “expected reproductive success” (Grafen, 1998; Goodman et al., 2012), and some researchers measure this in terms of levels of individual capital (i.e. different forms of wealth). Borgerhoff Mulder and Beheim (2011) (see also Borgerhoff Mulder et al., 2009) categorize three types — embodied, material, and relational capital. Each could have different relationships with fertility and parental investment depending on the economic context.

For example, lowering fertility can potentially raise an individual’s physical well-being, increasing their embodied capital (Kaplan et al., 1995; Kaplan, 1996). Somatic states like body mass, strength, and immune system could work as fitness-enhancing currencies (Kaplan et al., 1995) in a foraging niche. On the other hand, in market-based economies with low mortality and longer life expectancies, embodied capital such as knowledge and skills (which economists call “human capital”) are more valuable, contributing to an individual’s ability to thrive, find a partner, and potentially reproduce (Kaplan, 1996). This argument resonates strongly with economic theories on parents’ fertility decisions (Becker, 1960; Becker and Lewis, 1973) in industrial societies, and is viewed as the main driving force of the fertility decline.

In contrast to both foraging and market-dependant environments, pastoral and agricultural societies might rely relatively more on “material capital” (e.g. land, livestock, consumption goods, money), which can be stored, accumulated, and transferred to children across generations. This creates a positive correlation between wealth and fertility in pre-demographic transition societies (Borgerhoff Mul-

der, 1987; von Rueden et al., 2011). Because of the differences in the nature and value of different wealth currencies, this positive association is weaker in industrial settings (Nettle and Pollet, 2008; Hopcroft, 2006, 2015; Colleran et al., 2015).

260 Embodied and material capital can be “rival”, such that the amount of one type of capital transferred to one child is no longer available to another child. This might lead to diversification of offspring capital within a family. Such parental investment trade-offs could therefore diminish the benefits of having large numbers of children. In contrast, relational capital does not necessarily suffer this limitation. Parents’
265 social networks — whether for food-sharing, hunting or foraging, or other forms of help — can be shared among siblings and do not necessarily diminish with the number of children.

3.2 Wealth Inheritance and Intergenerational Mobility

Depending on the context and production mode, having more or fewer children may
270 be beneficial for parents in terms of wealth flows across generations. Caldwell (1976, 1978, 1982) highlighted that wealth does not always flow “down” the generations: it can in fact flow from children to parents via child labor, and that this is especially important under peasant farming or in traditional agricultural economies (Caldwell, 1978). High fertility can be beneficial in this context.

275 But when populations are becoming more market-integrated, both embodied and material capital can play different, complex roles in children’s success — reproductively or socio-economically. Theoretical models have shown that low fertility could coevolve with (material) wealth accumulation if reproductive success is tied to the amount of heritable wealth (Hill and Kern Reeve, 2005; Mace, 1996, 1998; Rogers, 1990) - this is important in economies with wealth transfers (dowry, brideprice) at
280 marriage. For example, Mace (1996, 1998) combined dynamic models with ethnographic data to show that the wealth requirements of both marriage and the costs of raising children can decrease optimal fertility to very low levels. Rogers (1990) similarly showed, assuming a different economic context, that long-term fitness could
285 theoretically be increased by lowering fertility in the short-run, though he was unable to obtain the same result in a more realistic model (Rogers, 1995a). Following Lack (1968), Grafen (1998) showed that if individuals differ in their reproductive value (i.e., expected reproductive success), parents should exhibit reproductive restraint to maximize the “value” of their children instead of the absolute number.
290 This pursuit of reproductive value generates a null or negative relationship between

wealth and fertility in post-demographic transitions (Grafen, 1998).

Empirically, studies that have tried to find long-term fitness advantages for low fertility have not been successful, though they do typically find evidence for wealth accumulation over successive generations (Kaplan et al., 1995; Mueller, 2001; Goodman et al., 2012). Yet in order for low fertility to be genetically advantageous, there must be a fitness payoff to having high-quality children over multiple generations. It is unclear at present how many generations should be considered, and whether children really differ in their reproductive value.

Lowering fertility for long-term reproductive success may be further driven by social stratification. Since the dilution of resources between large numbers of children increases the chances of downward intergenerational social mobility (i.e. ending up in a “lower” social class than one’s parents) in a stratified society, low fertility may be a strategy for avoiding this outcome and/or increasing the chances of upward social mobility (Lesthaeghe, 1977; Van Bavel, 2006; Van Bavel et al., 2011; Harpending and Rogers, 1990). Harpending and Rogers (1990) show that small family sizes have evolved to avoid downward social mobility when different social classes have differential reproductive outcomes. In their model, individuals in lower social strata could end up with lower long-term (i.e. multi-generational) fitness than individuals in higher strata, despite having more offspring in the first generation. Also, downward mobile individuals from the poorer stratum could end up in a “destitute” social class, or a “reproductive sink”, at the bottom of the hierarchy, without being able to reproduce (Harpending and Rogers, 1990). Thus, relatively poorer individuals can achieve higher long-term fitness by getting even one of their offspring into a higher social class. As a result, natural selection should favor poorer individuals who reduce fertility to invest in their offspring’s upward social mobility. In turn, the wealthy could reduce fertility to avoid downward social mobility due to the dilution of resources.

Harpending and Rogers (1990) claim that reproductive “destitution” of the sort assumed in their model would have existed in European cities during early demographic transitions, but individuals could have been removed from the reproductive pool via out-migration. Nevertheless, it is unclear whether such absolute destitution was or remains widespread in contemporary less developed countries, since the existence of modern social welfare systems may mitigate the risks of reproductive failure. Therefore, despite evidence of fertility limitation as a response to poverty (Gurmu and Mace, 2008), further data is needed to establish the existence of a

“reproductive sink” and a fitness disadvantage to downward social mobility.

Notwithstanding this caveat, there is an empirical association between family size and intergenerational mobility. In two studies of nineteenth century Belgium, Van Bavel and colleagues (2006; 2011) found that larger families experienced greater
330 dilution of resources, and individuals with larger numbers of siblings had higher chances of downward mobility, independent of parental social status and birth order. Although low fertility seems to be a way to avoid downward mobility for the wealthy and the middle classes, the same strategy is not used by the poor to gain upward mobility (Van Bavel et al., 2011).

335 Consistent with this, Skjærvø et al. (2011) show that among historical Norwegians in the early nineteenth century, women moving down a social class had significantly lower lifetime fertility than women who moved up from an initially lower social class. Also, women who maintain their position in the highest class had the highest lifetime fertility. In other words, downward mobility is more costly than
340 upward mobility is beneficial. This fits with the well-documented phenomenon that the wealthy tend to initiate fertility decline earlier and often more dramatically than the poor (Livi-Bacci, 1986).

3.3 Environmental Risks

Reproductive trade-offs are always subject to environmental changes. For example,
345 Winterhalder and Leslie (2002) and Leslie and Winterhalder (2002) argue that individual reproductive output is risk- or variance sensitive. That is, individuals may over-produce when mortality uncertainty is high and under-produce when it is low. Liu et al. (2012) similarly argue that fertility decline may be a response to the reduced risk of breeding failure (i.e. not raising any offspring to maturity)
350 rather than a direct response to mortality declines. As uncertainty about offspring survival to reproductive age goes down, the “required” threshold of fertility to avoid maternal “breeding failure” is also reduced. Using historical multi-generational data from Finland, they show that the number of children raised to reproductive age per mother remained relatively constant from 1880 to 1970. But since the reductions
355 in the risk of “breeding failure” preceded reductions in fertility, actual fertility was higher than “required” fertility in each decade. They estimated this risk to be extremely low even for women who began reproducing at a relatively late age and who had one child. This study suggests that reducing the risk of reproductive failure may play an important part in fertility decline.

360 Reduced fertility may also trade-off with greater survivorship under periodic environmental crises. Boone and Kessler (1999) show that if population history is characterised by climatic or other stochastic events, individuals can increase the probability of lineage survival by having fewer offspring and expending more on their surviving capacity or social status (see Low et al., 2002; Low et al., 2003, 365 and Shenk et al., 2016 for similar arguments). It is easy to imagine when resources become scarce or limited in a population bottleneck, access to them is likely to be inequitable and favor the wealthy and/or high status individuals (Low et al., 2002; Low et al., 2003, see also Boone and Kessler, 1999). Given the extreme climatic and environmental variation experienced during the Pleistocene, such bottlenecks are 370 plausible. However, stochastic fluctuations of such magnitude were unlikely since the Neolithic period, so the enormous increases in fertility during the Neolithic transition could represent a relaxation of this trade-off.

3.4 Social Interactions and Kinship

Reproductive decisions are not only about optimal energetic investments. They include strategic considerations within a social environment, and parents might adjust 375 their fertility decisions based on others' behavior. For example, Shenk et al. (2016) show that under high inequality and intense competition for status, higher parental investment in embodied capital and social status may lead to lower fertility. A number of theoretical models have also shown that competition between lineages for survival, rather than individual maximization of fitness, may be responsible for the 380 evolution of low fertility (Boone and Kessler, 1999; Grafen, 1998; Low et al., 2002; Hill and Kern Reeve, 2005). For example, Hill and Kern Reeve (2005) show that above the minimum threshold of investment (zero) needed to ensure offspring lineage success, a "snowballing resource competition" can develop between individuals 385 within a population. This leads to ever-increased investment in the resource-earning potential of ever-decreasing numbers of children.

Competition for heritable assets among siblings can also lead to low fertility (Kaplan, 1996; Kaplan et al., 2002; Lawson and Mace, 2009, 2010a, 2011). There is evidence that mental health (Lawson and Mace, 2010b), height (Lawson and Mace, 390 2008), educational achievement (Desai, 1995), and parental care (Lawson and Mace, 2009) are compromised by sibling competition in larger families. Producing fewer offspring may ensure survival (Hill and Kern Reeve, 2005; Boone and Kessler, 1999) and accommodate the increasing cost of having children in wealthier environments or

post-transition societies (Mace, 1998). On this interpretation, low fertility becomes
395 a strategy to reduce the dilution of resources and to alleviate sibling competition.

Sibling competition may also be exacerbated by the level of wealth or development in a society (Lawson and Mace, 2010a). HBEs have shown that in the early stages of demographic transition, wealthier families invest relatively more in “embodied” capital such as education, but they also begin to discriminate more between
400 children in their allocation of resources (Gibson and Sear, 2010). Sudden changes in land availability or rural development initiatives can also create novel competition between siblings for parental investment (Gibson and Gurmu, 2011). In wealthy populations where uncontested “basic” cushions against absolute poverty such as medical care and social welfare are available, competition between offspring for the
405 “surplus” resources in wealthy families may increase (Lawson and Mace, 2010a; Downey, 2001).

Reproductive outcomes are therefore often the result of negotiations between the conflicting reproductive interests of multiple kin, and should be understood within the “kinship ecology” (Leonetti et al., 2007; Leonetti and Nath, 2009) as a whole (see
410 Grafen, 1984). For example, siblings may act as non-reproductive “helpers at the nest”, forfeiting their own reproduction in assisting that of their siblings (Kramer, 2005, 2010; Crognier et al., 2001, 2002; Turke, 1988). Siblings may compete for limited parental resources that are necessary for their future reproductive success (Trivers, 1974), but this competition can be relaxed if extended kin step in to help
415 (reviewed in Sear and Mace, 2008). There may also be reproductive conflict between different generations of females who trade off their own reproduction for their daughters’ and daughters-in-law’s reproduction. This pattern may have led to the evolution of human menopause and post-reproductive lifespans (Lahdenperä et al., 2012; Mace and Alvergne, 2012; Cant and Johnstone, 2008; Volland and Beise, 2005).

Various kin may have differential reproductive and investment strategies, which are observable in the fertility outcomes of reproducing women (Sear and Coall, 2011; Sear and Mace, 2008, see also Fox et al., 2010). The general patterns indicate that maternal kin tend to be associated with increases in offspring “quality” and paternal kin with increases in offspring “quantity” (for review see Sear and Coall, 2011; Sear
425 and Mace, 2008).

Also, males and females may have evolved different reproductive and mating strategies (though see Moya et al., 2016 for a critique). A prominent explanation for these patterns centers on differences in paternity confidence and relatedness — they

experience different costs to reproduction, and have different levels of confidence in
430 their relatedness to their offspring, as a man can never be 100 percent certain that
his offspring are his own (Trivers, 1972).

Inclusive fitness theory implies that both direct and indirect reproduction (i.e.
enhancing the reproductive success of other related individuals) contribute to future
genetic representation in a population (Hamilton, 1964; Grafen, 1984). Empirically,
435 kin have been shown to have important effects on infant survival (reviewed in Sear
and Mace, 2008), female fertility (reviewed in Sear and Coall, 2011), and to some
extent, contraceptive use (Borgerhoff Mulder, 2009; Leonetti et al., 2007, though see
Mace et al., 2006; Mace and Colleran, 2009; Alvergne et al., 2011). Kin interactions
enable humans to outpace the reproduction of other great apes despite a shorter
440 reproductive window, and give rise to uniquely human life history characteristics
(elongated childhood, extensive allocare and lengthy post-reproductive lifespans).
Undeniably, kinship appears so important to our success as a species that many
now consider homo sapiens an obligate “cooperative breeder” (Alexander, 1974;
Hrdy, 1999; Hrdy, 2007; Hrdy, 2009; Mace and Sear, 2005; Sear and Mace, 2008;
445 though see Strassmann and Kurapati, 2010; Strassmann, 2011 for critique. See also
Clutton-Brock, 1991).

3.5 Summary

HBE is a powerful framework that has contributed significantly to our understand-
ing of reproductive behavior. At its core, the optimality model of human behavior
450 assumes that individuals are rational actors who make reproductive trade-offs based
on complete information and perfect cognitive capabilities (Colleran, *Forthcoming*).
Despite its strengths, some of the predictions made by the optimality model have
only limited empirical support (see Lawson and Mulder, 2016 for a review). For
example, the trade-offs between fertility and offspring survival or long-term repro-
455 ductive success may not always follow the patterns predicted by the model. Ad-
ditionally, measuring key concepts like reproductive value remains challenging. To
gain a deeper understanding of fertility transitions, future research needs to identify
which factors come into effect only in post-transitional era. By accounting for the
historical and cultural contexts that shape human behavior, researchers can build
460 more comprehensive models that better capture the complexity of human reproduc-
tive decision-making.

4 Cultural Evolution

CE studies social and behavioral changes due to information acquired from conspecifics in a population. Defined as socially transmitted information, culture
465 (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985), on this model, spreads via the interaction of various modes of transmission at the population level and learning biases at the individual level (Colleran, *Forthcoming*).

CE highlights different transmission modes, of which oblique and horizontal transmission is especially crucial in explaining low fertility behavior. Combined
470 with learning biases such as indirect and conformist biases, these can in principle accelerate the spread of the genetically maladaptive behavior that does not promote Darwinian fitness.

Unlike models assuming optimality at the individual level in HBE or economics, CE theory does not necessarily assume specific forms of utility or payoff functions
475 at the individual level. Instead, it looks at trait frequencies in the population and stresses more the structured (demographic or social) and constructed aspects of social environments (e.g., norms, values, and traditions) which operate at both the individual and group level.

4.1 Transmission Modes of Fertility Values

To illustrate how different modes of transmission affect demographic behaviour, we
480 can consider that women probably inherit reproductive behavior, values and norms initially from their parents, especially their mothers, via vertical transmission. Empirically, fertility and its intermediate indicators such as age at marriage and age at last birth are positively correlated between mothers and daughters (Anderton et al.,
485 1987; Murphy, 1999; Murphy and Wang, 2001; Reher et al., 2008; Jennings et al., 2012), and these associations are especially substantial in the post-demographic transition era (Murphy, 1999; Reher et al., 2008; Jennings et al., 2012). Although some argue this is a genetic process (Bocquet-Appel and Jakobi, 1993; Kohler et al., 1999; Madrigal et al., 2003; Blum et al., 2006; Pettay et al., 2005; Kosova et al.,
490 2010), numerous studies suggest that transmissions of reproductive-related values (e.g., ideal family size, contraceptive use), childrearing practices (e.g., prolonged breastfeeding) and childrearing environments (e.g., help from mothers or other family members) are important social mechanisms increasing observed intergenerational similarities (Jennings et al., 2012; Reher et al., 2008).

495 On reaching maturity, women are often exposed, via their social interactions,
to the reproductive norms of non-kin in their social environments (e.g. Balbo and
Barban, 2014; Colleran, 2020). In contrast to genetic inheritance, this allows oblique
and horizontal transmission of norms from non-parental individuals to additionally
shape behaviour. Since non-kin have no genetic stake in a woman’s reproductive
500 success according to inclusive fitness theory (Hamilton, 1964), they may be less
pronatal as compared to kin (Newson et al., 2005). Using a role-play experiment,
Newson et al. (2007) finds empirical support for a “kin influence hypothesis” (New-
son et al., 2005) — participants primed to role-play a mother were more pronatal
than those who were not.

505 Apart from reproductive attitude, oblique and horizontal transmissions also act
as channels for spreading knowledge and practices about contraceptive use (Gayen
and Raeside, 2010; Colleran and Mace, 2015; Kendal et al., 2005), health services,
childcare alternatives, or even the compatibility between parental roles and labor
force participation (Montgomery and Casterline, 1996). For example, during the
510 1950s, U.S. women were not expected to work until their children reached school
age. Along with industrialization and attitudinal change, it became more accept-
able for a woman to balance family and employment, and the percentage of parents
who believed “a pre-school kid is likely to suffer if his/her mother works” grad-
ually decreased over time (Rindfuss and Brewster, 1996). Without sound family
515 policies such as mandated paid leave, however, the incompatibility between labor
participation and childrearing responsibilities drove down fertility. It was not un-
til institutionalized childcare became widely available, allowing women to combine
work and parenthood, that the fertility rates started to climb.

4.2 Modernization

520 In explaining fertility transitions, it is crucial to highlight the role of modernization,
which brings tremendous structural change in social networks due to urbanization,
mass communication, commercial activities, migration, education and employment.
When non-kin/peers make up a higher proportion of individual social interactions,
their relative influence becomes more prominent. Non-kin are assumed by evolu-
525 tionary anthropologists to be less pronatal, opening up the possibility for them to
be the driving force of low fertility behavior in contemporary social networks (New-
son et al., 2005, 2007; Newson, 2009; Newson and Richerson, 2009; Colleran, 2020).
Compared to vertical transmission, oblique and horizontal transmission between

non-kin/peers have an asymmetric feature whereby one individual can transmit in-
530 formation to many individuals (Cavalli-Sforza and Feldman, 1981), and this can
make the spread of new cultural traits even more efficient in modern societies.

Prestige bias (Henrich and Gil-White, 2001) may be particularly important in
contemporary market economy, where individuals compete to attain higher social
status. The competitive environment of modernization creates opportunities for in-
535 dividuals in high-prestige positions, such as teachers, to become “social models” that
others imitate. This imitation is not limited to practices related to status-seeking,
such as education, but also extends to fertility-reducing behaviors that these indi-
viduals engage in to achieve their high status. This “indirect bias” (Cavalli-Sforza
and Feldman, 1981; Boyd and Richerson, 1985; Richerson and Boyd, 2005) indirectly
540 generates associations between fertility-limiting behavior and motivations to attain
high status, and becomes the driving force of the low-fertility norm. Combined
with the asymmetric (one-to-many) nature of oblique and horizontal transmission
described above, the prominence of these role models accelerates the effect even
further (see also Collier et al., 2014 on education).

545 4.3 Cultural Niche Construction

The above situation of prestige bias is a form of cultural niche construction, whereby
organisms alter their environments and consequently change the selection pressure
acting on them (Laland et al., 2001, 2007; Laland and Brown, 2006). Consider
the situation where a first cultural trait, such as a preference for education, is a
550 “background” factor, i.e. is distributed such that the mean is high. This back-
ground distribution can create the conditions for a second cultural trait, e.g. a
fertility-reducing preference, to spread through the population even though the sec-
ond trait might lead to lower average fitness (Ihara and W. Feldman, 2004). Kendal
et al. (2005) developed a model examining how the adoption of contraceptives could
555 evolve in such a “constructed” environment with a background preference among
individuals for education.

“Constructed” cultural niches such as this could have influence on transmission
probabilities even beyond local populations, which could lead to various onsets and
dynamics of fertility transition in different regions. A prominent feature of mod-
560 ern demographic transition is that while fertility rates decrease with development
(Notestein, 1953), the dynamics and pace vary substantially for different countries
(Bongaarts and Watkins, 1996). Less developed countries are experiencing earlier

onsets compared to historical context, due to the informational or ideational influence of neighboring more-developed countries, which have higher rates of acceptance of contraceptives or small-family norms (Bongaarts and Watkins, 1996; Amin et al., 2002). Extending Ihara and W. Feldman (2004), Borenstein et al. (2006) developed a metapopulation model to illustrate such a situation. In the metapopulation, each sub-population, or group, has its own background or context such as a particular average education level that can differentially facilitate the spread of low fertility in the group. In addition, the mean education in a group determined how sensitive the individuals were to the frequency of low fertility preferences in the metapopulation overall. In other words, the spread of low fertility in a particular group was influenced not only by the average education level in that group, but also by the overall education level and the prevalence of low fertility in the metapopulation as a whole. The model shows that because of the variation in education level between groups, low fertility spreads not only within but also between groups. This can explain why populations could experience fertility decline at different stages of economic development, even though the decline begins in wealthy populations at first (Bongaarts and Watkins, 1996; Borenstein et al., 2006).

These models advance our understanding of how contextual factors at the group level might influence the cultural transmission of low fertility. They highlight the interactive and multilevel quality of these dynamics, i.e. the feedback between individuals and higher levels of social organization. They also clearly show how group-level characteristics, such as average wealth or education, influence individual propensities to pursue a strategy of low fertility. These dynamics need to be reflected in empirical work (see Colleran et al., 2014; 2015 for example). While some models above assume structured populations (see also Fogarty et al., 2019; Deffner et al., 2022), socioeconomic strata might be impacted by the average wealth in a group differently, or individuals at different periods of life may use different learning strategies. Taking socioeconomic strata or age cohorts into account might further complicate the dynamics and probably alter the model outcomes.

4.4 Cultural Group Selection

An argument that is not yet explicitly made in the CE literature, is that low fertility could be culturally group selected (see Henrich, 2004). That is, low fertility, while maladaptive at the individual level, may be adaptive at the group level. For this to work, groups composed of individuals with low fertility should outcompete groups

composed of individuals with high fertility, and the advantage should be at the group and not necessarily the individual level.

An instance of this group level benefit of low fertility is from global economic development. One of the fundamental socioecological differences between pre- and post-industrialized societies is the extent to which populations interact with and depend on each other in international trade and supply networks (see Dang and Bauch, 2010, and references therein). Thus macro level competition and cooperation between populations or countries may have created a selective pressure for individuals within groups to invest in “embodied capital” and market-oriented skills, which are needed for the continued growth of the economy (Becker, 1994). Variation in the resource base and developmental trajectory of different countries (see Sachs, 2000) would then result in country-level variation in “reproductive equilibria”, on which cultural group selection could potentially act.

Lower fertility has been observed in wealthier (Bloom, 2011; Sinding, 2009, see also Mace, 2008) and market-dependent (Reher, 2012) groups, as the perceived investment needed for each child could be higher in those societies. For example, Moses and Brown (2003) find that there is a negative allometric relationship between national fertility rates and per capita energy consumption, coinciding with many biological laws (West et al., 1999; Peters, 1983). Increases in international trade have also been shown to have a negative effect on fertility rates within a country (Doces, 2011; Galor and Mountford, 2008). As countries become more dependent on technology and innovation for economic productivity, those that share international research and development (RD) and bilateral foreign direct investment (FDI) are more economically productive than those that do not cooperate in this way (Borensztein et al., 1998; Keller, 2000). The exchange of capital, technology, and labor thus effectively down-regulates each other’s fertility rates, as shown in theoretical models of population biology (Bauch, 2008; Dang and Bauch, 2010).

Cultural group selection operating on such between-group competition and cooperation is a theoretical possibility, e.g. countries that offer better living conditions might be more successful in spreading their values and gaining influence through attracting more migration (Richerson and Boyd, 2008). However, this hypothesis is as yet an untested one. Empirical evidence would require establishing what exactly groups are competing for, and whether the benefits of reducing fertility at the group level outweigh individual costs. It is also important to decipher whether such phenomena are simply driven by individual level selection. If individuals with lower

fertility simply do better on average than individuals with higher fertility, group level advantages would not be necessary to explain the phenomenon.

As Bongaarts and Watkins (1996) note, fertility decline is likely to be driven by a nested set of interactions. At the lowest level these would involve interactions between individuals living in social networks, kinship ecologies, socioeconomic classes, or communities, followed by interactions between communities themselves, and finally by interactions between countries in a global network. All of these levels should be investigated in future research.

5 Speaking with Social Sciences

5.1 The Divide

In the previous two sections, we have focused on how evolutionary theories offer first-principle explanations to fertility transition. And as we briefly mentioned in the beginning of the chapter, contemporary social sciences like demography, sociology, and economics have accumulated a huge amount of literature about the same topic, results which have appeared and been referenced in public discourse and policy. Evolutionary explanations for fertility transition are rarely referred to in traditional social sciences and public discussions. This evolutionary vs non-evolutionary divide (van den Berghe, 1990; Udry, 1995) is not unique to the topic of fertility transition, but extends to other subjects like socialization, social stratification, resource distribution, cooperation, warfare, etc (see for example Thayer, 2004; Takács, 2018). The reasons range from fears in many disciplines about the potential resurgence of Social Darwinism (Degler, 1991; Leyva, 2009) and/or misunderstandings about what contemporary evolutionary research concerns are (Colleran and Mace, 2011), resistance to evolutionary concepts (van den Berghe, 1990; Pinker, 2002; Ellis, 1996), limited exposure (Ellis, 1996; Thayer, 2004; Takács, 2018), and epistemological critiques (Bryant, 2004; Gould, 1981; Lewontin et al., 1984; Turner and Machalek, 2018).

There are two other reasons, as we view it, why the two sides do not speak to each other. First, the time scale of analysis and the level of resolution of research questions are distinctly different. Evolutionary theories, drawing on biological and anthropological research, consider humans as a species and often approach research questions from a cross-species comparative perspective. For evolutionary processes to operate, the considered time scale tends to be very long. In contrast, non-

evolutionary fields study relatively short-term and sometimes transient phenomena
665 embedded in various quite specific institutions, countries, and time periods. Although the human evolutionary sciences consider cross-cultural perspectives too, these tend to be studied either at a very low level of resolution in the case of phylogenetic studies, or are committed to focusing on subsistence societies that by definition exclude the vast majority of industrialised populations (e.g. the focus on
670 non-Western-Educated-Industrialised-Rich and Democratic/WEIRD societies (Henrich et al., 2010)). These differing emphases mean the research objects for the two sides are also dissimilar, with evolutionary fields focusing on small-scale and historical societies and non-evolutionary social sciences focusing more on industrialized, contemporary societies.

675 Second, many traditional social sciences differ fundamentally from the evolutionary sciences in their research motivations. While generally natural and evolutionary sciences look for descriptive statements, traditional social sciences such as economics and political science, although claiming to be observational and value-free, are strongly interested in policy implications. This policy-orientation is reflected in the selection of research topics and questions. For example, a climate
680 politics researcher might hope to mitigate global warming, and a labor economist who gauges effects of education or employment programs may be keen to give policy advice to governments to alleviate poverty. This shifts scholars' attention away from evolutionary, or purely theoretical, understandings of their research interests.

685 5.2 The Consequences

The consequences of this differentiation are parallel disciplines that do not engage each other. For example, (a)social learning and its macro-level outcomes is core business in cultural evolution. Theory specifies numerous learning mechanisms such as direct, indirect, or frequency-dependent biases. But in other fields like experimental
690 economics and behavioral game theory (see Camerer, 2003; Fudenberg and Levine, 1998, for general introduction), learning mechanisms are elaborated differently. Individuals make strategic decisions and adjustments to others in interactive environments according to learning rules like emulation dynamics (Ellison and Fudenberg, 1993; Fudenberg and Levine, 1998), belief learning (Cournot, 1838; Meese and Rogoff, 1983; Engel and West, 2005), fictitious play (Brown, 1951; Robinson, 1951;
695 Fudenberg and Kreps, 1995), weighted fictitious play (Cheung and Friedman, 1997), reinforcement learning (Bush and Mosteller, 1955; Luce, 1959; Suppes and Atkinson,

1960; Mookherjee and Sopher, 1997; Roth and Erev, 1995), experience-weighted attraction (EWA) Learning (Camerer and Hua Ho, 1999), imitation learning (Schlag, 1999), etc. These learning rules describe human cognition and decision-making in a more fine-grained way and could potentially offer complementary insights for cultural evolutionists.

The macro-patterns, e.g. of information transmission, that cultural evolutionists are interested in are also studied in adjacent fields. One of these is the s-shaped adoption curves generated (though not uniquely) by conformist transmission or positive frequency-dependence (Boyd and Richerson, 1985; Henrich and Gil-White, 2001), whereby individuals conform disproportionately as the majority trait in a population increases. A similar pattern is common in many other social and natural processes and is not unique to cultural change. Disease transmissions, the accumulation of crowd size in a social movement, the acceptance of international norms such as nuclear taboo, responsibility to protect (R2P), and human rights, all share the same dynamic, and have been discussed extensively in political science, sociology, public health, communication studies, etc. The literature we cited in the first section from economics, namely Spolaore and Wacziarg (2022) and Montgomery and Casterline (1996), attempt to describe this spreading process without referring to any evolutionary concept. By engaging in interdisciplinary conversations, cultural evolution could become a useful analytic framework for other research areas. Conversely, empirical case studies from a wide range of disciplines can also be harnessed to aid in the theoretical development of cultural evolution.

5.3 Scientific Implications

Social phenomena are notoriously difficult to measure, predict, and explain. When similar phenomena are triangulated via different scientific assumptions and disciplinary traditions, we can potentially be more confident in our general insights. However, isolated intellectual endeavors also create blind spots. Inter-disciplinary conversations are essential for identifying these. For example, reproductive decisions in HBE involve intergenerational fitness maximization and resource distribution concerns. But according to the “decision sciences” (e.g., psychology, behavioral economics, and neuroeconomics), humans discount benefits in the remote future and behave myopically (Frederick et al., 2002; Doyle, 2012; Odum, 2011), and there is a great deal of behavioral evidence for this (e.g. Thaler, 1981; Wang et al., 2016). The upshot is that, even were parents able to make optimized fertility plans, the

revealed behavior might not be consistent with any calculation, regardless of what level rationality is operated on. Indeed, numerous studies have found a mismatch between people’s fertility intentions and their actualized fertility (e.g. Müller et al., 735 2022). Figuring out how to reconcile findings from these areas might shed light on gaps as well as overlaps in different areas research on reproductive decisions.

There are benefits to going beyond disciplinary borders. Cultural evolution studies focus on culture transmissions that lead to aggregate changes. In modern societies, social media provides a great arena to study this kind of information spread. 740 The blossoming studies of computational social science using digital trace data to track mis/disinformation, political opinion, and hate speech might offer the exact same methodological tools for studying spread of fertility norms or other reproductive practices (although see Acerbi, 2020). One important question is how this modern environment of information spread differs from other small-scale, agricultural, traditional, or developing societies, and what its implications are for fertility 745 behavior. The challenge is to be specific about what exactly is being transmitted, given that we often can have multiple unmeasurable motivations for a single observed behavior (Colleran, 2016).

Being a theory oriented discipline, cultural evolution studies have generated quite 750 a few excellent models for explaining fertility transition (e.g. Ihara and W. Feldman, 2004; Bongaarts and Watkins, 1996). However, these models are less useful when applied empirically to specific regions, periods, subgroups, policy context, or countries where people respond to incentives differently. For instance, how do cultural evolutionary processes interact with different economic conditions (e.g., economic growth and hardship, developmental trajectories, labor markets, wealth distribution and 755 inequality), political factors (political systems, institutions, political stability (Feng et al., 2000), political attitude (Fieder and Huber, 2018)), social trends (e.g., migration), public policies (e.g., social welfare, parenting and childcare policy), and major historical events like pandemics, wars, baby booms, etc? While all of these events 760 can be understood as culturally niche-constructed, they are nonetheless different social phenomena occurring over different time scales and under different economic and historical contexts. To what extent can they be captured by our models?

Finally, transdisciplinary approaches can provide non-obvious interpretations. Fertility transitions are bio-social processes, and severe endogeneity problem makes 765 it extremely hard to parse causality from our observations. Fortunately, variations in institutions and policies (e.g., Gibson and Gurmu, 2011; Gibson and Lawson,

2011) that are implemented in different regions and subpopulations can also be seen as different treatment exposures in so-called “natural experiments”. With counterfactual and causal inference tools already used in economics (e.g., Cunningham, 2021; Huntington-Klein, 2022) and political science (e.g., Fearon, 1991; Tetlock and Belkin, 1996), along with clear study designs and conditional comparisons, we can begin to analyze our questions within the broader ecosystem of the social sciences.

6 Conclusion

Fertility transition is a complex phenomenon, part of our biological processes but also deeply intertwined with our social institutions. We have reviewed studies from anthropology, demography, and economics to outline some of the patterns of fertility transition. We then focused on attempts from human evolutionary ecology and cultural evolution to understand the outlined patterns, stressing the importance of both socioeconomic and socio-cultural interpretations. We highlighted that cultural evolution, as a multilevel framework, incorporates not only factors at individual and group levels, but also the feedback between them.

Taking inspiration from population genetics, the theoretically rich discipline of cultural evolution has laid out a unifying analytical framework, and has much to offer for studying interactions between fertility behavior and trends in human history and societies. An important direction for future work though is to discern if the insights produced by those theoretical explorations are reflected in our empirical world. This includes collecting multi-level data on social learning processes, inspecting the dynamics outlined in the models of cultural niche construction, and validating the concepts of cultural group selection. Guided by theoretical models, finer-grained data can in turn inform or modify our theory development to avoid the problems of equifinality (Premo, 2010), or underdetermination (Lake, 2015), and to verify our inferences. Cross-disciplinary conversation with other non-evolutionary social sciences will help cultural evolutionists engage more with how contemporary social issues interact with our fertility behavior.

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