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Evolutionary contributions to the study of human fertility

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Evolutionary contributions to the study of human fertility

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Demography, lacking an overarching theoretical framework of its own, has drawn on theories in many other social sciences to inform its analyses. The aim of this paper is to bring to the demographic community's attention research in the evolutionary sciences on fertility, and to demonstrate that evolutionary theory can be another useful tool in the demographer's toolkit. I first dispel some myths which impede the incorporation of evolutionary theory into demography: I make it clear that evolutionary explanations do not assume that all human behaviour is hardwired and functions to maximize genetic fitness; that they are able to explain variation in human behaviour; and that they are not necessarily alternatives to social science explanations. I then describe the diversity of work on fertility by evolutionary researchers, particularly human evolutionary ecologists and cultural evolutionists, and illustrate the usefulness of the evolutionary approach with examples of its application to age at first birth and the fertility transition.

Keywords: evolutionary demography; evolutionary anthropology; fertility; life history theory; human evolutionary ecology; cultural evolution

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Introduction

> Evolutionary demography is best viewed not as an alternative to traditional approaches but as a general theoretical framework that can inform and enhance existing research endeavors. (Kaplan and Lancaster 2003, p. 212)

My aim in contributing to this issue on the 'long view' of population is to describe how evolutionary theory can help inform studies of demographic patterns, particularly fertility. The theory that human behaviour and physiology have ultimately been shaped to maximize reproductive success allows testable hypotheses to be generated, and provides a coherent theoretical framework for analysing human demography. As the quote above from evolutionary anthropologists Hillard Kaplan and Jane Lancaster implies, this does not mean that it is the only theoretical framework which has value in explaining demographic behaviour; I concur with Burch (2003), who has argued that demographers need to become more comfortable with the idea of using several different theoretical models for the same phenomenon. Nor do I mean to suggest that all demographic behaviour functions to maximize reproductive success. However, given that the human species has evolved through the same process of natural selection as every other species, a complete and holistic understanding of why people have children and why they have the number of children that they do requires some input from evolutionary biology.

Demography and evolutionary biology have a long history (Kreager 2009; Sear 2015). As is well known, Darwin was influenced by Malthus when developing his ideas on natural selection in the mid-nineteenth century, and the two disciplines of demography and evolutionary biology remained closely associated into the early twentieth century. They diverged after the Second World War, with demography aligning itself firmly with the social, rather than biological, sciences. This was probably in part because of the desire to dissociate demography from the taint of eugenics, which significantly hampered the application of biology to the human sciences during the post-war period. Another factor may have been the very rapid changes in demographic patterns, particularly fertility, which were occurring in many countries, and which suggested that demographic behaviour had its basis in cultural rather than genetic change. Over the last few decades, the two disciplines have begun to reunite successfully (Carey and Vaupel 2005). Much of this new work in evolutionary demography has focused on the study of mortality, however (see e.g. Jones et al. 2014), and there is room for more interaction between the two disciplines in the study

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of fertility (but for some examples of explicitly evolutionary demographic work on fertility, see Low 1993; Rodgers and Kohler 2003; Wachter and Bulatao 2003). Here, I describe research that used an evolutionary framework which can contribute further to the understanding of fertility. I will start by outlining why evolutionary theory should become a useful part of the demographer's toolkit.

What can evolutionary biology offer demography?

Demography is an integral part of evolutionary biology (Metcalf and Pavard 2007). Evolutionary biologists work on the assumption that both physiology and behaviour have been shaped by natural selection to maximize fitness (see Ridley 2003 for a textbook introduction). Evolution by natural selection requires that (1) traits are heritable; (2) there is variation in those traits; and (3) that variation is related to differential reproductive success. If these three things hold then those traits which result in higher fitness will spread throughout the population. Fitness in evolutionary biology refers to the representation of genes in future generations: an individual is biologically 'fit' if he or she succeeds in getting many copies of his or her genes into subsequent generations relative to others in the same population. What individuals are actually maximizing is 'inclusive fitness'—the passing on of genes to future generations through not only their own reproduction but also by the impact of their behaviour on the reproduction of their genetic relatives (Hamilton 1964). A shorthand term used to define fitness is 'reproductive success', most frequently measured as the number of children surviving to reproductive maturity, and I will use this term to mean 'inclusive fitness' throughout. Reproductive success is a composite of mortality and fertility: individuals must survive long enough to reproduce and successfully raise their offspring to reproductive maturity. Note that 'maximizing' reproductive success does not always mean to produce as many offspring as physiologically possible. In many species, including our own, offspring require substantial investment from parents to become successful reproductive adults (Lawson and Mace 2011; Sear 2011). Acknowledging the central importance of reproductive success to evolutionary biology, Vaupel (1997) has suggested: '*If nothing in biology can be understood except in the light of evolution, an equally valid generalization is that nothing in evolution can be understood except in the light of demography* (p. 34).'

The dialogue should be two-way, however. Demography can benefit from greater integration with the evolutionary sciences, because they can add a valuable body of empirical work to demography. The top-down, theoretically motivated approach of evolutionary biology means that the human evolutionary sciences are very diverse, interdisciplinary, and comparative. In order to answer the theoretical questions that interest them, evolutionary scientists work on both physiological and behavioural aspects of fertility. They draw on anthropology and psychology as well as biology, and they take a comparative approach to fertility, including comparisons within and across species, and across populations. This approach can add a broader perspective to the 'object science' of demography, which tends to focus on empirical observations first and causal explanations later (Carey 1997; Coleman 2000). Most importantly, however, evolutionary biology can provide a theoretical framework to help interpret demographic phenomena. Demography has been described by its own practitioners as being a discipline without a theory (Wunsch 1995; Tabutin 2007), a concern (Crimmins 1993) that has led to the incorporation into the discipline of helpful theoretical frameworks from elsewhere, and such achievements as the successful union of economics and demography (Sigle-Rushton 2014), and the emergence of anthropological demography (Kertzer and Fricke 1997; Coast et al. 2007).

Evolutionary biology is another theoretical framework which has the ability to generate new hypotheses and fresh ideas, and lead to a more holistic understanding of demographic phenomena (Carey and Vaupel 2005; Wachter 2008). Demography is the most biological of the social sciences, dealing with the processes of birth and death, and therefore evolutionary theory is an obvious candidate to become one of those useful theoretical frameworks which demographers call upon. We have evolved through exactly the same process of natural selection as has every other species. It is vanishingly unlikely that human demographic processes can be explained entirely without reference to evolved physiological and behavioural mechanisms. If a *holistic*, complete understanding of demographic processes at every level is required, then evolutionary theory must be included as part of the framework.

With respect to fertility, there is still much that is not understood by demographers about what shapes fertility levels and trends. Here, theoretical frameworks can be enormously useful in helping fill in the gaps in understanding. Further, the question of 'why do people have children?' appears to be only answerable by including an evolutionary perspective. Children score

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relatively badly when it comes to helping their parents maximize the benefits that people are typically supposed to maximize—health (Ronsmans and Graham 2006), wealth (Kaplan 1994), and happiness (Kohler et al. 2005). Yet the majority of individuals still choose to have children, even in societies where they have free access to effective methods of contraception (Coleman 2000; Morgan and King 2001). The only possible explanation is that we have evolved physiological and behavioural mechanisms which result in the production of children, despite the high costs involved, because that is the primary way to achieve reproductive success.

What is evolutionary demography and what is it not?

I will define evolutionary demography as the application of evolutionary theory to demography. Starting with the assumption that physiology and behaviour have largely been shaped by natural selection to maximize fitness, testable hypotheses can be generated to inform our understanding of demographic patterns. The assumption that human demographic patterns can be explained using an evolutionary framework is still somewhat controversial, since it is often assumed within the social sciences that humans' reliance on social learning and cultural transmission of behaviours has resulted in our behaviour becoming entirely decoupled from fitness considerations. I believe this viewpoint stems from several misunderstandings of the evolutionary approach, which I will now attempt to dispel.

Evolutionary demographers are not genetic determinists

The first misconception is that any trait which has a genetic basis is fixed and immutable. This is problematic for many social scientists since it does not fit with empirical observations of the flexibility of human behaviour. It is true that an evolutionary approach entails a commitment to the hypothesis that there is some genetic basis to the traits under study (both physiological and behavioural traits), but it does not follow that such traits are rigidly determined by genes. An individual's phenotype (her observable physiological and behaviour traits) is determined by the interaction of her genotype with her environment. Evolutionary demographers therefore do not consider human traits to be fixed and immutable, but instead assume that they can be influenced by a change in environment; in biological jargon, this characteristic is known as phenotypic plasticity. This plasticity has arisen through natural selection to allow individuals to respond adaptively to the environment. It is not entirely unconstrained and unpredictable, but flexible in predictable ways. For example, in well-nourished populations, girls reach menarche relatively early; in poorly nourished populations, average age at menarche is later. However, there is still a relatively narrow range of ages at which girls reach menarche: there is no population where the average age of menarche is either 30 years or 3 years of age (Morabia and Costanza 1998).

The evolutionary research I describe below is mostly agnostic about the exact nature of the link between genes and phenotype; this approach is known in biological jargon as the 'phenotypic gambit' (Grafen 1984). Some social scientists are perfectly happy with the idea that there is some link between genes and physiology, and that natural selection may have shaped human physiology, but argue that human *behaviour* is entirely determined by social learning and has therefore been severed from genetic influence. This argument suggests that behavioural aspects of fertility are beyond the remit of the evolutionary sciences. I disagree: natural selection shapes behaviour just as it does physiology, and evolutionary demography allows for the influence on its shaping of both environment and social learning. This view is illustrated in Figure 1, which compares the standard social science model of how human behaviour is transmitted between generations to that of the contemporary evolutionary behavioural sciences. The evolutionary approach takes into consideration both the genetic and social transmission of behaviour. In social animals, learning from other individuals may be the most efficient mechanism for matching behaviour to the environment (Rendell et al. 2010). It may be easier, for example, for a chimpanzee to learn how to make a fishing rod for termite fishing by watching and copying the behaviour of another chimpanzee, rather than for every chimpanzee to reinvent the process of turning a branch into a termite fishing rod (Whiten 2005; Whiten et al. 2007). Social learning is then a mechanism by which adaptive behaviour can be brought about.

Evolutionary demographers are not blindly adaptationist

Another popular misconception is that evolutionists blindly assume that every human trait is perfectly adapted to its current environment as a means of achieving the goal of maximizing reproductive

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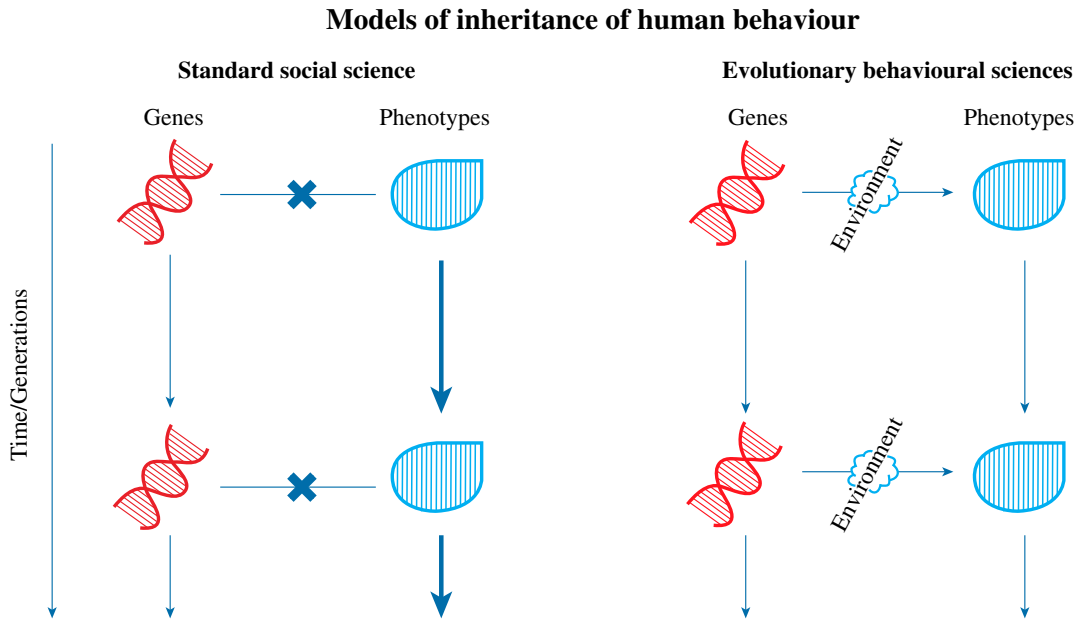

Figure 1 Two models of the transmission of human behaviour: the standard social science model and the model of contemporary evolutionary behavioural science
Source: Redrawn from Brown et al. 2011.

success. This seems incompatible with empirical observations which appear to show that some human behaviour is maladaptive. However, no evolutionary biologist assumes that all traits are perfectly formed adaptations to current environments. First, there are processes which influence the evolution of traits other than natural selection. 'Evolution' simply means change over time. Evolutionary biologists assume that natural selection is the mechanism by which most traits have arisen, but still allow for evolution within populations caused by other processes. 'Genetic drift' is the process by which gene frequencies change in populations simply by chance, for example. Transmission of behavioural traits through social learning is another process which can lead to shifts away from adaptive behaviour, since socially learned behaviours have the potential to mutate and spread more rapidly than genetic change through populations. Second, there are a variety of constraints which may prevent the ideal adaptation arising. For example, natural selection has to build on the characteristics already present in an organism, and cannot create perfect adaptations from scratch. Third, a recent change in environment may lead to previously adaptive behaviour becoming maladaptive in the new environment. This may be particularly relevant to our species, given the rapid changes in our environment that we have orchestrated in recent centuries.

The acknowledgement that not all human traits are adaptations to current environments does not mean an evolutionary approach is worthless. The assumption that most human traits evolved as adaptations designed to increase fitness in past environments is a valuable heuristic to use as a *starting point* when studying many facets of demography. Even in low-fertility societies, where individuals do not seem to be maximizing their fitness, our demographic behaviour may still be influenced by mechanisms which were adaptive in the past. Social learning arose via natural selection, and our brains—which are the organs that make social learning possible—have been shaped by millennia of natural selection to produce adaptive behaviour. Further, we can use evolutionary ideas to explore why individuals are no longer maximizing their fitness. If we assume that our behaviour has been shaped to maximize fitness in past environments, we can ask what particular environmental changes have led to a mismatch between our evolved psychological mechanisms and current environments.

Typically, then, while they adopt an overarching theoretical framework which assumes that most human traits have been shaped by natural selection, evolutionary demographers are not interested in testing whether a particular trait is adaptive. Instead, they use that overarching framework to test specific hypotheses derived from it, such as the hypothesis that factor X is correlated with fertility in some particular environment. If support is not found for the hypothesis, details of it are reconsidered, but the evolutionary framework is not necessarily abandoned

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(Parker and Maynard Smith 1990). There are some exceptions, the obvious one being for the fertility transition. It is an evolutionary puzzle that fertility begins to decline as wealth increases in populations all across the world, because according to evolutionary theory, individuals would direct any resources they have towards maximizing their reproductive success (Borgerhoff Mulder 1998). Evolutionists have been actively engaged in exploring this puzzle (Kaplan et al. 2002; Shenk 2009), and many of their analyses would be very familiar to mainstream demographers. Thus, in their studies of fertility behaviour, evolutionists have investigated the role of the economic costs and benefits of children (Lawson and Mace 2009, 2011; Gibson and Sear 2010); and of cultural transmission (Mace et al. 2006; Alvergne et al. 2011) and of both (Borgerhoff Mulder 2009; Shenk et al. 2013; Snopkowski and Kaplan 2014). Some of this analysis is less common in demography: evolutionists have actively explored, empirically (Kaplan et al. 1995; Goodman et al. 2012) and mathematically (McNamara and Houston 2006), whether such behaviour may be adaptive in terms of long-term lineage fitness, and have proposed that our evolved predispositions towards accumulating wealth and status are misfiring in current environments, where large family sizes adversely affect the accumulation of resources (Borgerhoff Mulder 1998). Even if behaviour is not adaptive (that is, directed to maximizing reproductive success) in its current environment, it can still be studied within an evolutionary framework.

Evolutionary demographers do not ignore human diversity

The misconception that evolutionists are only interested in explaining the evolution of species-typical traits may lead to the assumption that evolutionary demographers have nothing of interest to say to social scientists, who are frequently interested in explaining variation in human traits. Some human evolutionary research is indeed concerned with species-typical traits, for example, work on the evolutionary puzzle of the menopause—the question of why women become unable to produce any more children just halfway through their potential lifespans (Hawkes et al. 1998; Shanley and Kirkwood 2001; Shanley et al. 2007; Alberts et al. 2013). However, most of the human evolutionary sciences are explicitly engaged in explaining human diversity, for the obvious reason that there is considerable variation in our species to explain. In fact, the key to our success as a species may be our behavioural flexibility, enabling us to colonize a range of environments, using a range of different subsistence strategies (Wells and Stock 2007).

Evolutionary demographers do not assume that individuals are consciously trying to maximize their reproductive success

One problem for evolutionists working on our species is that their subjects have the ability to reflect on their own behaviour. An objection frequently made against evolutionary theories is that it is blatantly obvious that the desire for genetic representation in future generations is not a conscious rationale that motivates any human behaviour. This objection hinges on the very big assumption that human fertility behaviour is driven by conscious decision-making. Evolutionists are typically agnostic on this point. Every other species manages to maximize its reproductive success without conscious decision-making, and clearly, humans must be able to do the same. When evolutionary scientists use agentic terms such as ‘strategies’, therefore, this is not intended to refer to conscious strategies.

Evolutionary explanations are not necessarily alternatives to social scientific explanations

Perhaps the largest impediment to the integration of the evolutionary and social sciences is the assumption that evolutionary and social sciences are engaged in a zero-sum game, and that evolutionary and social scientific explanations are alternatives that cannot coexist (Carey and Vaupel 2005). However, to propose an evolutionary explanation for a given phenomenon is not to claim that any explanation provided by social science is necessarily invalid. Traits can be explained at several different levels. Evolutionary explanations stem from an interest in explaining the ‘ultimate’ function of that trait in evolutionary terms: how does (or did) this trait serve to maximize fitness? The same trait can also be explained by proximate explanations: what are the processes (behavioural, cultural, societal) which bring about this particular trait? Much social science focuses on these proximate explanations without being interested in whether the observed behaviour serves an ultimate function in maximizing reproductive success. Many evolutionists are also interested in studying proximate mechanisms, but their research is guided by the assumption that the mechanisms are or were driven by an ultimate, fitness-maximizing motivation. Sometimes evolutionary and social science theories

do make different predictions, and explicitly testing alternative hypotheses against one another can prove extremely fruitful in moving forward our understanding of a particular behaviour (Kaplan 1994). However, for much of the time, evolutionary and social scientists are interested in explaining behaviour at different levels (ultimate vs. proximate), so that many social science explanations for behaviour in no way obviate the possibility that there may also be an ultimate explanation for the behaviour, in terms of it maximizing that individual's fitness.

Evolutionary approaches to fertility

In this section I will briefly describe evolutionary approaches to the study of fertility, concentrating on research which has focused on the second and third requirements of natural selection: investigations of how *phenotypic* traits differ between individuals and how this variation is linked to differential reproductive success. Most of this work is by evolutionary behavioural scientists, though not all the work I describe can be considered behavioural science since many evolutionists are comfortable moving between behavioural and physiological aspects of fertility (see Laland and Brown 2011 for an introduction to the evolutionary behavioural sciences; see also Wilson 1999 and Barthold et al. 2012 for examples of demographers bringing evolutionary theory into their work on fertility).

Some work on demographic phenomena has explicitly attempted to identify links between genes and phenotypes. For example, the field of behavioural genetics attempts to quantify the heritability of traits, frequently using twin studies (Hughes and Burleson 2000). Work in this area has suggested that a number of demographically relevant traits are partly genetically inherited. These include age at first birth, age at first attempt to have children and number of children, and also traits linked to fertility, such as age at menarche and sexual behaviour (see reviews in Rodgers et al. 2000; Kohler et al. 2006; but see Vetta and Courgeau 2003 for a critique). A number of previous articles have made the case for the inclusion of genetic research in demography and related social sciences (Freese et al. 2003; Hobcraft 2006), so here I will describe only work done on fertility by evolutionary scientists investigating this issue phenotypically. I will divide this research into that which has focused on questions of function (how does this trait serve to maximize fitness?) and that which has focused on mechanism (what are the physiological, psychological, and cultural mechanisms which bring about the trait under study?).

Questions of function: what factors are correlated with fertility?

There has been a considerable amount of research in the evolutionary social sciences directly analysing fertility, most of it undertaken by human evolutionary ecologists (human behavioural ecologists is a more commonly used term, but this only refers to the study of behaviour. I use here the broader term of human evolutionary ecology, which includes the study of both behavioural and physiological traits). This branch of the evolutionary sciences is interested in investigating adaptive behaviour and physiology in its ecological context (see Smith 1992; Winterhalder and Smith 2000; Nettle et al. 2013 for overviews), that is, investigating the function of particular traits (where function means the purpose for which a trait evolved). Here ecological context is interpreted in the broadest possible sense to mean not just the physical environment but social and cultural context too. Human evolutionary ecology puts particular emphasis on ecological (= environmental) influence and how this interacts with the genotype to produce phenotypes, and is therefore particularly interested in explaining human variation. The bread and butter of human evolutionary ecology is the investigation of what causes variation in reproductive success, to the extent that it has been given the nickname within the evolutionary sciences of 'baby-counting'. This is a particularly rich area, then, for demographers to look for inspiration and points of common interest in the study of fertility.

The main theoretical framework of human evolutionary ecology is life history theory (Stearns 1992, 2000; Roff 2002), the branch of evolutionary theory concerned with the allocation of energy over an individual's life course, and how this energy is allocated between the main functions of survival, reproduction, and growth. It is based on the principle of allocation, which states that energy used for one purpose cannot be used for any other purpose. This principle leads to the expectation of trade-offs. For example, trade-offs are expected between survival and reproduction, and between growth and reproduction. Energy devoted to reproduction must then be divided: between that devoted to obtaining a mate or mates and that invested in offspring; between current and future offspring; and between quantity and quality of offspring. Though life history theory is framed in terms of energetic allocation

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between traits, the outcomes of these trade-offs are frequently observed at the behavioural level. Further, there is growing recognition of the importance of social, particularly intergenerational, transfers in the evolution of life history patterns (Kaplan and Robson 2002; Chu and Lee 2006). Each human, for example, relies not only on his or her own energy budget to survive and reproduce but also receives energy transfers from others, a phenomenon described in some of the evolutionary literature as a 'pooled energy budget' (Kramer and Ellison 2010).

From this framework of life history theory, predictions are derived and then tested against data (see Table 1 for examples). Thus most of the day-to-day work of those human evolutionary ecology researchers interested in fertility comprises the analysis of variation in fertility—an activity very familiar to many demographers. There are some differences in methodology. Many practitioners of human evolutionary ecology are evolutionary anthropologists, much of whose work on fertility has focused on the analysis of data, which the researchers may have collected themselves, from small-scale, subsistence-level societies. Often these data sets are large and longitudinal, and have the advantage of providing a rich array of data on relatively homogeneous populations (for an early and excellent example of evolutionary demography, see Hill and Hurtado 1996). As well as the differences, there are also many similarities between the methods of human evolutionary ecology and demography. There is a growing trend for human evolutionary ecology to make use of the kind of large-scale, nationally representative data sets familiar to demographers (Nettle et al. 2013), and there has always been a small sub-section of the community working on historical data (Voland 2000). Again, just like demographers, evolutionary scientists in this area occasionally make use of formal modelling approaches to explore their predictions. Further, human evolutionary ecologists have used this framework to develop conceptual models of fertility. Some of the most important evolutionary demography work on fertility has been produced by Kaplan and co-workers, who have used evolutionary theory to provide overarching models of fertility variation (e.g., Kaplan 1996; Kaplan et al. 2002; Kaplan and Lancaster 2003).

There is now a large literature on fertility from human evolutionary ecology. Table 1 lists some examples of questions asked by evolutionary social scientists, with an indication of the methods and settings they have used to answer the questions. Life history theory has a lot to say about the timing of fertility, so that many of these questions relate not just to variation in total fertility, but also to other components of fertility, particularly age at first birth. These examples illustrate the breadth of human evolutionary ecology research on fertility. Some questions focus on physiology (for example, is a trade-off visible between growth and age at first birth, that is, do girls who are taller in adulthood have later first births than those who are shorter?). Others are classic life history trade-off questions (are there trade-offs between fertility and child survival, or between current and future reproduction?). Yet others are questions familiar to many social scientists on relationships between socio-economic factors and fertility (do wealthier individuals have higher fertility? Do girls who suffer socio-economic adversity in childhood have earlier first births?). While some of these questions may be familiar to social scientists, their aetiology may differ. For example, questions on whether kin influence fertility stem from a hypothesis currently popular in evolutionary anthropology that humans are 'cooperative breeders', that is, that mothers require help to raise expensive human children, either from fathers of their children and/or other members of their family and social group (Hrdy 2005, 2009; Kramer 2010).

Questions of mechanism: what physiological, psychological, or cultural mechanisms cause fertility to vary?

Human evolutionary ecology is interested in the distal or ultimate explanations of fertility patterns, but tends to ignore the mechanisms through which variation in fertility may be brought about. There are other sections of the evolutionary human sciences interested in exploring these proximate mechanisms, which can broadly be divided into sub-disciplines interested in physiological, psychological, and cultural (i.e., social learning) mechanisms.

One sub-discipline, reproductive ecology, is the study of how reproductive physiology responds to its ecological context, and is particularly focused on the hormonal regulation of fertility (Ellison 2003; Vitzthum 2008). Reproductive ecology is a largely empirical discipline, which also uses the framework of life history theory, and its research has been guided by the expectation of trade-offs such as that between survival and reproduction. For example, it has shown that female reproductive hormones calibrate reproduction to energy availability by responding to both energy balance and energy 'flux', a measure of the rate of energy change (see Table 1), thereby ensuring that reproduction is only attempted when the extra energetic demands of pregnancy and lactation will

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Table 1 A selection of studies on fertility from the evolutionary social sciences

Research question	Methods	Setting	Reference
Questions concerning function: what factors influence fertility?			
Do wealthier men and women have higher fertility, and does this relationship vary across populations?	Analysis of both large- and small-scale survey data	Numerous high- and low-income settings	Reviews in Low (2000); Nettle and Pollet (2008)
Do development interventions which lighten women's workloads increase fertility?	Analysis of small-scale survey data	(1) Ethiopian agro-pastoralists, (2) Mexican agriculturalists	(1) Gibson and Mace (2002, 2006), (2) Kramer and McMillan (1999)
Is there a trade-off between current and future reproduction?	Analysis of longitudinal small-scale survey data	Gambia	Sear et al. (2003b)
Do kin influence fertility outcomes?	Analysis of small-scale, historical, and nationally representative data	(1) Gambia, (2) historical Poland, (3) UK British Household Panel Survey	(1) Sear et al. (2003a), (2) Tymicki (2004), (3) Mathews and Sear (2013a, 2013b)
Does childhood adversity correlate with earlier first births?	Analysis of nationally representative data	UK (1) Millennium Cohort Study, (2) National Child Development Survey	(1) Nettle (2010), (2) Nettle et al. (2011)
Do short women have relatively early first births?	Analysis of large-scale and small-scale survey data	(1) USA, Wisconsin Longitudinal Study, (2) Finland, (3) Gambia	(1) Stulp et al. (2012), (2) Helle (2008), (3) Allal et al. (2004)
Is polygyny correlated with fertility?	Analysis of small-scale survey and historical data	(1) Kenyan agro-pastoralists, (2) Tsimane forager-farmers, (3) historical Utah	(1) Borgerhoff Mulder (1989), (2) Winking et al. (2013), (3) Josephson (2002)
Is there a trade-off between fertility and child survival, and what factors affect its magnitude?	Analysis of both small-scale survey and nationally representative data	(1) Malian agriculturalists, (2) Ghana, (3) 27 sub-Saharan Demographic and Health Surveys	(1) Strassmann and Gillespie (2002), (2) Meij et al. (2009), (3) Lawson et al. (2012)
Does paying child support reduce men's subsequent fertility?	Analysis of nationally representative data	USA, Panel Study of Income Dynamics	Anderson (2011)
Are the economic costs and benefits of children, ecological risk factors, or cultural transmission better predictors of fertility in transitioning populations?	Analysis of survey data	(1) India, (2) Bangladesh	(1) Shenk (2009), (2) Shenk et al. (2013)
Does male contribution to diet in traditional societies increase fertility?	Population-level analysis	161 foraging societies	Marlowe (2001)
Is subsistence strategy correlated with fertility?	Population-level analysis	Numerous subsistence-level societies	Bentley et al. (1993)
When to have another baby?	Mathematical model, based on household wealth and existing family size and gender composition	Model based on parameters derived from survey of North Kenyan pastoralists	Mace (1996)
Questions concerning mechanism			
Physiological			
Does ovarian function vary with ecological conditions?	Hormonal assays	Multi-country study, including high- and low-fertility populations	Ellison et al. (1993)

Table 1 (*Continued*)

Research question	Methods	Setting	Reference
Does the age-related decline in testosterone vary between populations?	Hormonal assays	Multi-country study (USA, Congo, Nepal, Paraguay)	Ellison et al. (2002)
Are breast-feeding practices or maternal energy budget stronger correlates of the resumption of postpartum fecundity?	Hormonal assays	Argentina	Valeggia and Ellison (2004)
Are reproductive hormones negatively correlated with energetic expenditure (even in the absence of low energy intake)?	Hormonal assays	Polish farmers	Jasienska and Ellison (1998)
Does developmental experience influence levels of reproductive hormones in adulthood?	Hormonal assays, making use of natural experiment of international migration	Bangladesh and UK	Núñez de la Mora et al. (2007)
Are testosterone levels lower in partnered men and fathers than in non-partnered, non-fathers?	Hormonal assays of (1) cross-sectional, (2) longitudinal data	(1) Numerous studies in both high- and low-fertility countries, (2) Philippines	(1) Reviewed in Gray and Campbell (2009), (2) Gettler et al. (2011)
Do anovulation rate and early pregnancy loss vary seasonally?	Hormonal assays	Bolivia	Vitzthum (2009a)
Psychological			
Do women or men experience 'baby fever', a conscious longing for children?	(1) Qualitative analysis, (2) analysis of survey data	Finland	(1) Rotkirch et al. (2012), (2) Rotkirch (2007)
Does personality influence fertility?	Analysis of survey data	(1) USA, (2) Senegal	(1) Jokela et al. (2011), (2) Alvergne et al. (2010)
Does mortality priming increase fertility intentions?	(1) Internet experiment, (2) lab experiment	(1) UK university students, (2) US university students	(1) Mathews and Sear (2008), (2) Griskevicius et al. (2011)
Is exposure to the deaths of acquaintances or close friends/family associated with lower intended or actual age at first birth?	Online (SocialSci) survey	USA	Pepper and Nettle (2013)
Does an interest in infants mediate the relationship between socio-economic environment and adolescent girls' intended timing of first reproduction?	Small-scale survey	UK adolescents	Clutterbuck et al. (2014)
Cultural			
Do social norms become less pro-natal as societies modernize and social networks become less kin-oriented?	(1) Conceptual model, tested with (2) lab experiment of social influences on reproductive attitudes	(2) UK	(1) Newson et al. (2005), (2) Newson et al. (2007)
Does contraceptive uptake spread through friendship or spatial networks?	Analysis of cross-sectional survey	Ethiopia	Alvergne et al. (2011)
Does cultural niche construction influence the spread of fertility norms?	Mathematical models		Ihara and Feldman (2004); Kendal et al. (2005)
Does community-level education accelerate fertility decline?	Analysis of small-scale survey data	Rural Poland	Colleran et al. (2014)

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not prove too costly to the woman's own health. It is also a field, somewhat unusual in reproduction research, which has not neglected men: there is now a substantial body of research on how both female and male reproductive hormones vary between and within societies (Bribiescas 2001; Vitzthum 2009b). Reproductive ecology has also explored the predicted trade-off between mating and parental effort by testing whether men's hormonal profiles respond to partnering and fatherhood, finding evidence that testosterone may mediate a shift from mating effort to parenting effort in men (Gray and Campbell 2009).

Another sub-discipline, evolutionary psychology, is the branch of psychology which assumes that the mind has been shaped by natural selection (Dunbar and Barrett 2007; Swami 2011). To understand fertility behaviour at all levels, an understanding of the proximate psychological mechanisms which drive fertility decisions is needed (Hobcraft 2006). So far there has been little research in evolutionary psychology on fertility. There is a substantial literature on mate preferences, which are relevant to fertility, but there have been few attempts to link research on mate preferences to partnership choices or fertility decisions (Sefcek et al. 2007). There have, however, been a handful of studies which have shed some light on evolved psychological mechanisms surrounding reproduction (see Table 1). Evolutionary psychology is an almost entirely empirical discipline, and is also unusual among the evolutionary social sciences in focusing largely on what are known in the discipline as WEIRD populations: Western, Educated, Industrialized, Rich and Democratic (Henrich et al. 2010). While some research has used surveys to explore possible psychological mechanisms which influence fertility—such as correlations between personality traits and fertility—much psychological research uses methods less known in demography, including laboratory-based or Internet-based experimental research.

Finally, some researchers in the field of cultural evolution (Whiten et al. 2011) are interested in how social learning and cultural influences affect fertility (see Table 1 for examples). This interest was evident in some of the earliest works in cultural evolution, which suggested that cultural transmission could help explain the fertility transition (Cavalli-Sforza and Feldman 1981). This is the area of the evolutionary social sciences most comfortable with the idea that human behaviour can be decoupled from classic Darwinian natural selection. As well as being interested in how behaviours are learned socially, researchers in this field also study how cultures evolve (through a process analogous to, but not necessarily driven by, genetic evolution (Mesoudi et al. 2004)), and some espouse the idea of selection at the level of the cultural group, not just the gene (Boyd and Richerson 2002; Henrich 2004). Some researchers in the field are also interested in feedback loops between behaviour and both genetic and cultural change. Known as 'niche construction', this is the idea that humans (or other animals) are able to change their own selection pressures by changing their environment; new adaptations then arise to fit this new environment, either through genetic or cultural change (Laland et al. 2001).

This field has clear parallels in some of the demographic literature on the cultural spread of low fertility, but cultural evolution also has the ability to provide some fresh insights on fertility. For example, cultural evolutionary research on social learning is interested both in *how* people learn from others and *what* they learn from others. Unlike the blank-slate model favoured by some social scientists, which assumes that babies are born capable of learning pretty much anything, cultural evolution considers how social learning is constrained by both content biases (so what we learn is not random) and transmission biases (so how we learn is not random) (Rendell et al. 2011). Common transmission biases are considered to be (1) prestige bias, which makes us more likely to learn from prestigious or high-status individuals, and (2) conformity biases, which makes us likely to copy the most common behaviour. Both biases are thought to stem from adaptive heuristics. For example, learning from high-status individuals may result in the acquisition of behaviours which lead to high status. These prestige transmission biases have been proposed as part of the explanation of fertility decline (Boyd and Richerson 1985). This hypothesis was proposed as a conceptual model, which has been modelled mathematically but not tested empirically, as is true of much cultural evolution work on fertility. Clearly there is the potential for dialogue between demographers and cultural evolutionists on how the empirical expertise of demographers could be harnessed to test the models of cultural evolution (see Mesoudi and Whiten 2008 for examples of how empirical work on transmission biases has been used in other areas of cultural evolution). This may be a particularly beneficial area for collaboration between social and evolutionary scientists, since cultural evolution works on the very social processes of key concern to so many social sciences.

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How might evolutionary research on fertility be used to inform demography?

Table 1 demonstrates that many of the questions evolutionary demographers ask, and the methods they use, are similar to those common in demography, though evolutionary demography also has some different interests and methods. Empirically, then, evolutionary demography can add pieces to the solution of the puzzle of why fertility varies. It can also add to the diversity of knowledge on fertility given the ability of evolutionary demography to move across disciplines (across the physiological, psychological, and cultural causes of fertility variation) and across different kinds of population, from low-population-density, subsistence-level, high-fertility communities to high-density, high-income, and low-fertility populations. The concern of evolutionary demographers with ultimate function can also help provide a unifying and holistic framework which answers questions to which demographers as yet have no answer, though in some cases this may be because they have not yet asked the question.

Broadly speaking, evolutionary demography is interested in asking 'why' questions, whereas demography is interested in 'how' questions. There are times when evolutionary biology may be able to fill in gaps by taking a step back to understand why demographic phenomena are patterned as they are, rather than how variation in demographic phenomena is brought about. This was the case in the study of mortality, when demographers turned to biologists to help them explain the puzzle of mortality patterns at advanced ages, which standard demographic methods cannot account for (Vaupel 1997). To give a fertility example, demographic research on the cultural transmission of fertility has been criticized for providing only a mechanism by which low fertility spreads through social networks, but not explaining *why* low fertility should arise and spread (Pollak and Watkins 1993). The cultural evolutionists Boyd and Richerson (1985) have proposed that prestige bias may be part of the answer to this question. The typically positive relationship between status and fertility may reverse in modernizing populations, for example, if lengthy periods in education become necessary to achieve status, so that only individuals with few children achieve it. Prestige bias may then result in other individuals copying the low fertility of high-status individuals, thus leading to the spread of low fertility.

An evolutionary perspective may also help explain why other social science models sometimes fail to fully explain human behaviour, perhaps because humans behave in ways that do not appear to be 'rational', such as not always maximizing wealth or well-being. Natural selection has ultimately shaped us to maximize our genetic fitness, which may sometimes lead to behaviour which will not maximize health or wealth. For example, in contemporary industrialized populations, there is a clear link between low socio-economic status or childhood adversity and early childbearing. One school of thought suggests that early childbearing is likely to damage the potential to invest in one's own education and employment prospects (McLanahan 2004), implying that early childbearing should be discouraged. On the other hand, a line of evolutionary research considers that early childbearing is perfectly rational within a fitness-maximizing framework, as a strategic response to indicators of adversity, which in past environments would have been correlated with a high risk of dying before being able to successfully complete reproduction (Johns et al. 2011; Nettle 2011).

There are also times when evolutionary biology may be able to provide an extra layer of explanation which unifies existing work, and yields a holistic account of fertility variation. For example, economic demographers are largely content with models of fertility which assume that individuals will maximize some utility based on cost–benefit functions, though exactly what utility is being maximized may vary between models. An evolutionary perspective can add a further layer of explanation by proposing that the utility which individuals are ultimately maximizing is fitness, and that other utility-maximization rules (of which there may be many) evolved in the service of maximizing fitness.

Conclusion

This brief survey has only been able to scratch the surface of work relevant to fertility in the human evolutionary sciences, but I hope it has demonstrated that much work of interest to demographers exists. If the research is unfamiliar to many demographers this may be because relatively little of it has been published in demography journals or conducted by researchers who see themselves as demographers. This survey should have demonstrated that evolutionary demography is not just interested in physiological processes or biomarkers, but that the evolutionary social sciences can contribute significantly to an understanding of how social and cultural processes shape demographic patterns too. Perhaps the key difference between evolutionary and demographic approaches is that demography is

a 'bottom-up' discipline, primarily interested in data (and much data description and analysis can be done without reference to theory), while evolutionary biology is a 'top-down', theoretically motivated discipline (in which data are a means to an end—Kaplan and Gurven 2008). Despite these different approaches, there are questions in which both disciplines are interested, so that greater communication between evolutionary and demographic researchers has the potential to be of mutual benefit, and eventually to yield a holistic understanding of how and why fertility varies between and within populations.

Notes

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References

Alberts, S. C., J. Altmann, D. K. Brockman, M. Cords, L. M. Fedigan, A. Pusey, T. S. Stoinski, K. B. Streier, W. F. Morris, and A. M. Bronikowski. 2013. Reproductive aging patterns in primates reveal that humans are distinct, *Proceedings of the National Academy of Sciences of the United States of America* 110(33): 13440–13445.

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

Alvergne, A., M. Jokela, and V. Lummaa. 2010. Personality and reproductive success in a high-fertility human population, *Proceedings of the National Academy of Sciences* 107(26): 11745–11750.

Alvergne, A., M. A. Gibson, E. Gurmu, and R. Mace. 2011. Social transmission and the spread of modern contraception in rural Ethiopia, *PLoS ONE* 6(7): e22515.

Anderson, K. G. 2011. Does paying child support reduce men's subsequent marriage and fertility?, *Evolution and Human Behavior* 32(2): 90–96.

Barthold, J. A., M. Myrskylä, and O. R. Jones. 2012. Childlessness drives the sex difference in the association between income and reproductive success of modern Europeans, *Evolution and Human Behavior* 33(6): 628–638.

Bentley, G. R., T. Goldberg, and G. Jasienska. 1993. The fertility of agricultural and non-agricultural societies, *Population Studies* 47(2): 269–281.

Borgerhoff Mulder, M. 1989. Marital status and reproductive performance in Kipsigis women: re-evaluating the polygyny-fertility hypothesis, *Population Studies* 43(2): 285–304.

Borgerhoff Mulder, M. 1998. The demographic transition: are we any closer to an evolutionary explanation?, *Trends in Ecology and Evolution* 13(7): 266–270.

Borgerhoff Mulder, M. 2009. Tradeoffs and sexual conflict over women's fertility preferences in Mpimbwe, *American Journal of Human Biology* 21(4): 478–487.

Boyd, R. and P. J. Richerson. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R. and P. J. Richerson. 2002. Group beneficial norms can spread rapidly in a structured population, *Journal of Theoretical Biology* 215(3): 287–296.

Bribiescas, R. G. 2001. Reproductive ecology and life history of the human male, *Yearbook of Physical Anthropology* 116(33): 148–176.

Brown, G., T. E. Dickins, R. Sear, and K. N. Laland. 2011. Evolutionary accounts of human behavioural diversity, *Philosophical Transactions of the Royal Society B, Biological Sciences* 366: 313–324.

Burch, T. K. 2003. Demography in a new key: a theory of population theory, *Demographic Research* 9(11): 263–284.

Carey, J. R. 1997. What demographers can learn from fruit fly actuarial models and biology, *Demography* 34(1): 17–30.

Carey, J. R. and J. W. Vaupel. 2005. Biodemography, in D. L. Poston and M. Micklin (eds.), *Handbook of Population*. New York: Kluwer Academic Press, pp. 625–658.

Cavalli-Sforza, L. L. and M. W. Feldman. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton, NJ: Princeton University Press.

Chu, C. Y. C. and R. D. Lee. 2006. The co-evolution of intergenerational transfers and longevity: an optimal life history approach, *Theoretical Population Biology* 69(2): 193–201.

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Clutterbuck, S., J. Adams, and D. Nettle. 2014. Childhood adversity accelerates intended reproductive timing in adolescent girls without increasing interest in infants, *PLoS ONE* 9(1): e85013.

Coast, E., K. Hampshire, and S. Randall. 2007. Disciplining anthropological demography, *Demographic Research* S5 (16): 493–518.

Coleman, D. 2000. Demography in intellectual context: a subject in search of a home, in Z. Pavlik (ed.), *The Position of Demography among other Disciplines*. Prague: Department of Demography and Geodemography, Charles University, pp. 27–35.

Colleran, H., G. Jasienska, I. Nenko, A. Galbarczyk, and R. Mace. 2014. Community-level education accelerates the cultural evolution of fertility decline, *Proceedings of the Royal Society B: Biological Sciences* 281(1779): 20132732.

Crimmins, E. M. 1993. Demography: the past 30 years, the present, and the future, *Demography* 30(4): 579–591.

Dunbar, R. I. M. and L. Barrett. 2007 *Oxford Handbook of Evolutionary Psychology*. Oxford: Oxford University Press.

Ellison, P. T. 2003. *On Fertile Ground: A Natural History of Human Reproduction*. Boston: Harvard University Press.

Ellison, P. T., C. Panter-Brick, S. F. Lipson, and M. T. Orourke. 1993. The ecological context of human ovarian function, *Human Reproduction* 8(12): 2248–2258.

Ellison, P. T., R. G. Bribiescas, G. R. Bentley, B. C. Campbell, S. F. Lipson, C. Panter-Brick, and K. Hill. 2002. Population variation in age-related decline in male salivary testosterone, *Human Reproduction* 17(12): 3251–3253.

Freese, J., J.-C. A. Li, and L. D. Wade. 2003. The potential relevances of biology to social enquiry, *Annual Review of Sociology* 29(1): 233–256.

Gettler, L. T., T. W. McDade, A. B. Feranil, and C. W. Kuzawa. 2011. Longitudinal evidence that fatherhood decreases testosterone in human males, *Proceedings of the National Academy of Sciences* 108(39): 16194–16199.

Gibson, M. and R. Mace. 2002. The impact of labor-saving technology on first birth intervals in rural Ethiopia, *Human Biology* 74(1): 111–128.

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

Gibson, M. A. and R. Sear. 2010. Does wealth increase parental investment biases in child education? Evidence from two African populations on the cusp of the fertility transition, *Current Anthropology* 51(5): 693–701.

Goodman, A., I. Koupil, and D. W. Lawson. 2012. Low fertility increases descendant socioeconomic position but reduces long-term fitness in a modern post-industrial society, *Proceedings of the Royal Society B: Biological Sciences* 279(1746): 4342–4351.

Grafen, A. 1984. Natural selection, kin selection and group selection, in J. R. Krebs and N. B. Davies (eds.), *Behavioural Ecology*. 2nd ed. Oxford: Blackwell, pp. 62–84.

Gray, P. B. and B. C. Campbell. 2009. Human male testosterone, pair-bonding and fatherhood, in P. T. Ellison and P. B. Gray (eds.), *Endocrinology of Social Relationships*. Cambridge, MA: Harvard University Press, pp. 270–293.

Griskevicius, V., A. W. Delton, T. E. Robertson, and J. M. Tybur. 2011. Environmental contingency in life history strategies: the influence of mortality and socioeconomic status on reproductive timing, *Journal of Personality and Social Psychology* 100(2): 241–254.

Hamilton, W. D. 1964. The genetical evolution of social behaviour I, *Journal of Theoretical Biology* 7(1): 1–16.

Hawkes, K., J. F. O'Connell, N. G. Blurton Jones, H. Alvarez, and E. L. Charnov. 1998. Grandmothering, menopause and the evolution of human life histories, *Proceedings of the National Academy of Sciences, USA* 95(3): 1336–1339.

Helle, S. 2008. A tradeoff between reproduction and growth in contemporary Finnish women, *Evolution and Human Behavior* 29(3): 189–195.

Henrich, J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation, *Journal of Economic Behavior and Organization* 53(1): 3–35.

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

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

Hobcraft, J. 2006. The ABC of demographic behaviour: How the interplays of alleles, brains, and contexts over the life course should shape research aimed at understanding population processes, *Population Studies* 60(2): 153–187.

Hrdy, S. B. 2005. Cooperative breeders with an ace in the hole, in E. Voland, A. Chasiotis, and W. Schiefenhoevel (eds.), *Grandmotherhood: The Evolutionary Significance of the Second Half of Female Life*. New Brunswick, NJ: Rutgers University Press, pp. 295–317.

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

Hughes, K. and M. Burleson. 2000. Evolutionary causes of genetic variation in fertility and other fitness components, in J. Rodgers, D. Rowe, and W. Miller (eds.), *Genetic Influences on Human Fertility and Sexuality*. Boston: Kluwer Academic Publishers, pp. 7–33.

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Ihara, Y. and W. Feldman. 2004. Cultural niche construction and the evolution of small family size, *Theoretical Population Biology* 65(1): 105–111.

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

Johns, S., T. Dickins, and H. Clegg. 2011. Teenage pregnancy and motherhood: How might evolutionary theory inform policy?, *Journal of Evolutionary Psychology* 9(1): 3–19.

Jokela, M., A. Alvergne, T. V. Pollet, and V. Lummaa. 2011. Reproductive behavior and personality traits of the five factor model, *European Journal of Personality* 25(6): 487–500.

Jones, O. R., A. Scheuerlein, R. Salguero-Gomez, C. G. Camarda, R. Schaible, B. B. Casper, J. P. Dahlgren, J. Ehrlein, M. B. Garcia, E. S. Menges, P. F. Quintana-Ascensio, H. Caswell, A. Baudisch, and J. W. Vaupel. 2014. Diversity of ageing across the tree of life, *Nature* 505(7482): 169–173.

Josephson, S. C. 2002. Does polygyny reduce fertility?, *American Journal of Human Biology* 14(2): 222–232.

Kaplan, H. 1994. Evolutionary and wealth flows theories of fertility: empirical tests and new models, *Population and Development Review* 20(4): 753–791.

Kaplan, H. S., J. B. Lancaster, J. A. Bock, and S. E. Johnson. 1995. Does observed fertility maximize fitness among New-Mexican men: a test of an optimality model and a new theory of parental investment in the embodied capital of offspring, *Human Nature* 6(4): 325–360.

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

Kaplan, H. S. and A. J. Robson. 2002. The emergence of humans: the coevolution of intelligence and longevity with intergenerational transfers, *Proceedings of the National Academy of Sciences of the United States of America* 99(15): 10221–10226.

Kaplan, H., J. B. Lancaster, W. T. Tucker, and K. G. Anderson. 2002. Evolutionary approach to below replacement fertility, *American Journal of Human Biology* 14(2): 233–256.

Kaplan, H. and J. Lancaster. 2003. An evolutionary and ecological analysis of human fertility, mating patterns and parental investment, in K. W. Wachter and R. A. Bulatao (eds.), *Offspring: Human Fertility in Biodemographic Perspective*. Washington, DC: National Academies Press, pp. 170–223.

Kaplan, H. and M. Gurven. 2008. Top-down and bottom-up research in biodemography, *Demographic Research* 19(44): 1587–1602.

Kendal, J. R., Y. Ihara, and M. W. Feldman. 2005. Cultural niche construction with application to fertility control: a model for education and social transmission of contraceptive use. Morrison Institute Working Paper Series 102.

Kertzer, D. I. and T. Fricke. 1997. Toward an anthropological demography, in D. I. Kertzer and T. Fricke (eds.), *Anthropological Demography: Toward a New Synthesis*. Chicago: University of Chicago Press, pp. 1–35.

Kohler, H. P., J. R. Behrman, and A. Skytthe. 2005. Partner plus children = happiness? The effects of partnerships and fertility on well-being, *Population and Development Review* 31(3): 407–445.

Kohler, H. P., J. L. Rodgers, W. B. Miller, A. Skytthe, and K. Christensen. 2006. Bio-social determinants of fertility, *International Journal of Andrology* 29(1): 46–53.

Kramer, K. L. and G. P. McMillan. 1999. Women's labor, fertility, and the introduction of modern technology in a rural Maya village, *Journal of Anthropological Research* 55(4): 499–520.

Kramer, K. L. 2010. Cooperative breeding and its significance to the demographic success of humans, *Annual Review of Anthropology* 39(1): 417–436.

Kramer, K. L. and P. T. Ellison. 2010. Pooled energy budgets: resituating human energy -allocation trade-offs, *Evolutionary Anthropology* 19(4): 136–147.

Kreager, P. 2009. Darwin and Lotka: two concepts of population, *Demographic Research* 21(16): 469–502.

Laland, K. N. and G. R. Brown. 2011. *Sense and Nonsense: Evolutionary Perspectives on Human Behaviour*. Oxford: Oxford University Press.

Laland, K. N., J. Odling-Smee, and M. W. Feldman. 2001. Cultural niche construction and human evolution, *Journal of Evolutionary Biology* 14(1): 22–33.

Lawson, D. W. and R. Mace. 2009. Trade-offs in modern parenting: a longitudinal study of sibling competition for parental care, *Evolution and Human Behavior* 30(3): 170–183.

Lawson, D. W. and R. Mace. 2011. Parental investment and the optimization of human family size, *Philosophical Transactions of the Royal Society B: Biological Sciences* 366(1563): 333–343.

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

Low, B. S. 1993. Ecological demography: a synthetic focus in evolutionary anthropology, *Evolutionary Anthropology* 1(5): 177–187.

Low, B. S. 2000. Sex, wealth and fertility: old rules, new environments, in L. Cronk, N. Chagnon, and W. Irons (eds.), *Adaptation and Human Behaviour: An Anthropological Perspective*. New York: Aldine de Gruyter, pp. 323–343.

Mace, R. 1996. When to have another baby: a dynamic model of reproductive decision-making and evidence

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from Gabbra pastoralists, *Ethology and Sociobiology* 17(4): 263–273.

Mace, R., N. Allal, R. Sear, and A. Prentice. 2006. The uptake of modern contraception in a Gambian community: the diffusion of an innovation over 25 years, in J. C. K. Wells, S. S. Strickland, and K. N. Laland (eds.), *Social Information Transmission and Human Biology*. Boca Raton, FL: CRC Press, pp. 191–205.

Marlowe, F. 2001. Male contribution to diet and female reproductive success among foragers, *Current Anthropology* 42(5): 755–760.

Mathews, P. and R. Sear. 2008. Life after death: an investigation into how mortality perceptions influence fertility preferences using evidence from an internet-based experiment, *Journal of Evolutionary Psychology* 6(3): 155–172.

Mathews, P. S. and R. Sear. 2013a. Does the kin orientation of a British female's social network influence her entry into motherhood?, *Demographic Research* 28(11): 313–340.

Mathews, P. S. and R. Sear. 2013b. Family and fertility: kin influence on the progression to a second birth in the British Household Panel Study, *PLoS ONE* 8(3): e56941.

McLanahan, S. 2004. Diverging destinies: how children are faring under the second demographic transition, *Demography* 41(4): 607–627.

McNamara, J. M. and A. I. Houston. 2006. State and value: a perspective from behavioural ecology, in J. C. K. Wells, S. S. Strickland, and K. N. Laland (eds.), *Social Information Transmission and Human Biology*. Boca Raton, FL: CRC Press, pp. 59–88.

Meij, J. J., D. Van Bodegom, J. B. Ziem, J. Amankwa, A. M. Polderman, T. B. L. Kirkwood, A. J. M. De Craen, B. J. Zwaan, and R. G. J. Westendorp. 2009. Quality-quantity trade-off of human offspring under adverse environmental conditions, *Journal of Evolutionary Biology* 22(5): 1014–1023.

Mesoudi, A., A. Whiten, and K. N. Laland. 2004. Is human cultural evolution Darwinian? Evidence reviewed from the perspective of the origin of species, *Evolution* 58(1): 1–11.

Mesoudi, A. and A. Whiten. 2008. The multiple roles of cultural transmission experiments in understanding human cultural evolution, *Philosophical Transactions of the Royal Society B: Biological Sciences* 363(1509): 3489–3501.

Metcalf, C. J. E. and S. Pavard. 2007. Why evolutionary biologists should be demographers, *Trends in Ecology and Evolution* 22(4): 205–212.

Morabia, A. and M. C. Costanza. 1998. International variability in ages at menarche, first livebirth, and menopause, *American Journal of Epidemiology* 148(12): 1195–1205.

Morgan, S. P. and R. B. King. 2001. Why have children in the 21st century? Biological predisposition, social coercion, rational choice, *European Journal of Population* 17 (1): 3–20.

Nettle, D. and T. V. Pollet. 2008. Natural selection on male wealth in humans, *The American Naturalist* 172(5): 658–666.

Nettle, D. 2010. Dying young and living fast: variation in life history across English neighborhoods, *Behavioral Ecology* 21(2): 387–395.

Nettle, D. 2011. Flexibility in reproductive timing in human females: integrating ultimate and proximate explanations, *Philosophical Transactions of the Royal Society B: Biological Sciences* 366(1563): 357–365.

Nettle, D., D. A. Coall, and T. E. Dickins. 2011. Early-life conditions and age at first pregnancy in British women, *Proceedings of the Royal Society B: Biological Sciences* 278(1712): 1721–1727.

Nettle, D., M. A. Gibson, D. Lawson, and R. Sear. 2013. Human behavioural ecology: current research and future prospects, *Behavioural Ecology* 24(5): 1031–1040.

Newson, L., T. Postmes, S. E. G. Lea, and P. Webley. 2005. Why are modern families small? Toward an evolutionary and cultural explanation for the demographic transition, *Personality and Social Psychology Review* 9(4): 360–375.

Newson, L., T. Postmes, S. E. G. Lea, P. Webley, P. J. Richerson, and R. McElreath. 2007. Influences on communication about reproduction: the cultural evolution of low fertility, *Evolution and Human Behavior* 28(3): 199–210.

Núñez-de la Mora, A., R. T. Chatterton, O. A. Choudhury, D. A. Napolitano, and G. R. Bentley. 2007. Childhood conditions influence adult progesterone levels, *PLoS Medicine* 4(5): e167.

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

Pepper, G. V. and D. Nettle. 2013. Death and the time of your life: experiences of close bereavement are associated with steeper financial future discounting and earlier reproduction, *Evolution and Human Behavior* 34(6): 433–439.

Pollak, R. A. and S. C. Watkins. 1993. Cultural and economic approaches to fertility: proper marriage or mesalliance, *Population and Development Review* 19(3): 467–496.

Rendell, L., R. Boyd, D. Cownden, M. Enquist, K. Eriksson, M. W. Feldman, L. Fogarty, S. Ghirlanda, T. Lillecrap, and K. N. Laland. 2010. Why copy others? Insights from the social learning strategies tournament, *Science* 328(5975): 208–213.

Rendell, L., L. Fogarty, W. J. E. Hoppitt, T. J. H. Morgan, M. M. Webster, and K. N. Laland. 2011. Cognitive culture: theoretical and empirical insights into social

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learning strategies, *Trends in Cognitive Sciences* 15(2): 68–76.

Ridley, M. 2003. *Evolution*. Oxford: Oxford University Press.

Rodgers, J. L., D. C. Rowe, and W. B. Miller. 2000. *Genetic Influences on Human Fertility and Sexuality: Theoretical and Empirical Contributions from the Biological and Behavioral Sciences*. Boston, MA: Kluwer Academic Press.

Rodgers, J. L. and H. P. Kohler. 2003. *The Biodemography of Human Reproduction and Fertility*. Boston, MA: Kluwer Academic Publishers.

Roff, D. A. 2002. *Life History Evolution*. Sunderland, MA: Sinauer Associates.

Ronsmans, C. and W. J. Graham. 2006. Maternal mortality: who, when, where, and why, *The Lancet* 368(9542): 1189–1200.

Rotkirch, A. 2007. 'All that she wants is a(nother) baby'? Longing for children as a fertility incentive of growing importance, *Journal of Evolutionary Psychology* 5(1): 89–104.

Rotkirch, A., S. Basten, H. Vaisanen, and M. Jokela. 2012. Baby longing and men's reproductive motivation, *Vienna Yearbook of Population Research* 2011: 283–306.

Sear, R. 2015. Evolutionary demography: a Darwinian Renaissance in demography, in J.D. Wright (ed.), *International Encyclopedia of the Social and Behavioural Sciences*, 2nd ed. Amsterdam: Elsevier.

Sear, R., R. Mace, and I. A. McGregor. 2003a. The effects of kin on female fertility in rural Gambia, *Evolution and Human Behavior* 24(1): 25–42.

Sear, R., R. Mace, and I. A. McGregor. 2003b. A life-history approach to fertility rates in rural Gambia: evidence for trade-offs or phenotypic correlations?, in J. L. Rodgers and H. P. Kohler (eds.), *The Biodemography of Human Reproduction and Fertility*. Boston: Kluwer Academic Publishers, pp. 135–160.

Sear, R. 2011. Parenting and families, in V. Swami (ed.), *Evolutionary Psychology: A Critical Introduction*. Oxford: Wiley-Blackwell, pp. 215–250.

Sefcek, J. A., B. H. Brumbach, G. Vasquez, and G. F. Miller. 2007. The evolutionary psychology of human mate choice, *Journal of Psychology and Human Sexuality* 18(2–3): 125–182.

Shanley, D. P., and T. B. L. Kirkwood. 2001. Evolution of the human menopause, *Bioessays* 23(3): 282–287.

Shanley, D. P., R. Sear, R. Mace, and T. B. L. Kirkwood. 2007. Testing evolutionary theories of menopause, *Proceedings of the Royal Society B: Biological Sciences* 274(1628): 2943–2949.

Shenk, M. K. 2009. Testing three evolutionary models of the demographic transition: changes in fertility and age at marriage in urban South India, *American Journal of Human Biology* 21(4): 501–511.

Shenk, M. K., M. C. Towner, H. C. Kress, and N. Alam. 2013. A model comparison approach shows stronger support for economic models of fertility decline, *Proceedings of the National Academy of Sciences* 110(20): 8045–8050.

Sigle-Rushton, W. 2014. *Fertility and Family Policy: An Intersectional, Feminist Perspective*. The Family Kaleidoscope: evolving partnerships and parenting, Universitair Centrum Sint-Ignatius Antwerpen.

Smith, E. A. 1992. Human behavioural ecology: I, *Evolutionary Anthropology* 1(1): 20–25.

Snopkowski, K. and H. Kaplan. 2014. A synthetic biosocial model of fertility transition: testing the relative contribution of embodied capital theory, changing cultural norms, and women's labor force participation, *American Journal of Physical Anthropology* 154(3): 222–233.

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

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

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

Stulp, G., S. Verhulst, T. V. Pollet, and A. P. Buunk. 2012. The effect of female height on reproductive success is negative in western populations, but more variable in non-western populations, *American Journal of Human Biology* 24(4): 486–494.

Swami, V. 2011. *Evolutionary Psychology: A Critical Introduction*. Oxford: Wiley-Blackwell.

Tabutin, D. 2007. Whither demography? Strengths and weaknesses of the discipline over 50 years, *Population* 62(1): 15–31.

Tymicki, K. 2004. The kin influence on female reproductive behaviour: the evidence from the reconstitution of Bejsce parish registers, 18th-20th centuries, Poland, *American Journal of Human Biology* 16(5): 508–522.

Valeggia, C. and P. T. Ellison. 2004. Lactational amenorrhea in well-nourished Toba women of Formosa, Argentina, *Journal of Biosocial Science* 36(5): 573–595.

Vaupel, J. W. 1997. Trajectories of mortality at advanced ages, in K. W. Wachter and C. E. Finch (eds.), *Between Zeus and the Salmon: The Biodemography of Longevity*. Washington, DC: National Academy Press, pp. 17–37.

Vaupel, J. 2003. Biodemography, in P. Demeny and G. McNicoll (eds.), *Encyclopedia of Population*. New York: Thomson Gale, pp. 84–87.

Vetta, A. and D. Courgeau. 2003. Demographic behaviour and behaviour genetics, *Population* 58(4): 401–428.

Vitzthum, V. J. 2008. Evolutionary models of women's reproductive functioning, *Annual Review of Anthropology* 37(1): 53–73.

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Vitzthum, V. 2009a. Modulation of reproductive effort during early pregnancy in humans, *American Journal of Human Biology* 21(4): 548–558.

Vitzthum, V. J. 2009b. The ecology and evolutionary endocrinology of reproduction in the human female, *American Journal of Physical Anthropology* 140(S49): 95–136.

Voland, E. 2000. Contributions of family reconstitution studies to evolutionary reproductive ecology, *Evolutionary Anthropology* 9(3): 134–146.

Wachter, K. W. 2008. Biodemography comes of age, *Demographic Research* 19(40): 1501–1512.

Wachter, K. W. and R. A. Bulatao. 2003. *Offspring: Human Fertility in Biodemographic Perspective*. Washington, DC: National Academies Press.

Wells, J. C. K. and J. T. Stock. 2007. The biology of the colonizing ape, *American Journal of Physical Anthropology* 134(S45): 191–222.

Whiten, A. 2005. The second inheritance system of chimpanzees and humans, *Nature* 437(7055): 52–55.

Whiten, A., A. Spiteri, V. Horner, K. E. Bonnie, S. P. Lambeth, S. J. Schapiro, and F. B. M. de Waal. 2007. Transmission of multiple traditions within and between Chimpanzee groups, *Current Biology* 17(12): 1038–1043.

Whiten, A., R. A. Hinde, K. N. Laland, and C. B. Stringer. 2011. Culture evolves, *Philosophical Transactions of the Royal Society B: Biological Sciences* 366(1567): 938–948.

Wilson, C. 1999. Evolutionary theory and historical fertility change, *Population and Development Review* 25(3): 531–541.

Winking, J., J. Stieglitz, J. Kurten, H. Kaplan, and M. Gurven. 2013. Polygyny among the Tsimane of Bolivia: an improved method for testing the polygyny–fertility hypothesis, *Proceedings of the Royal Society B: Biological Sciences* 280(1756): 2012–3078.

Winterhalder, B. and E. A. Smith. 2000. Analyzing adaptive strategies: human behavioral ecology at twenty-five, *Evolutionary Anthropology* 9(2): 51–72.

Wunsch, G. 1995. God has chosen to give the easy problems to the physicists, or why demographers need theory. Plenary address given at the European Population Conference, Milan, Italy, 4–8 September 1995.

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