Research Article

When not to have another baby:
An evolutionary approach to low fertility

Ruth Mace

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Ruth Mace[1]

Abstract

BACKGROUND
In this paper, I explain the theoretical foundations of fertility from the perspective of evolutionary demography and evolutionary anthropology.

OBJECTIVE
My goal in this paper is to provide examples of how evolutionary demography is generating and testing new hypotheses about human fertility and parental behaviour.

METHODS
To illustrate the paradigm of low fertility, I present several evolutionary explanations for reduced fertility, or no fertility at all. The explanations I cite are drawn from studies on child maltreatment, homosexual preference, post-demographic transition low fertility, and late-life low fertility (menopause), as these are phenomena that appear to challenge evolutionary approaches.

CONCLUSIONS
I find that the sophisticated tools of behavioural ecology and evolutionary anthropology and demography can do more than simply explain high fertility, and are currently being used to generate and test new hypotheses about fertility, including hypotheses that address the issue of low fertility.

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1. An introduction to evolutionary demography

Evolutionary demography (or the application of evolutionary theory to human demographic behaviour) rests on the assumption that all organisms are designed by natural selection. As evolutionary theory is an overarching theory that explains how all living things look, develop, and behave, it is not surprising that it is relevant to understanding human fertility. Natural selection is assumed to act on physiological and decision-making processes in such a way that these processes maximise inclusive fitness in the environment in which they evolved. Inclusive fitness is a measure of the number of relatives an individual produces, weighted according to how closely related they are to the individual by direct descent (Hamilton 1964).

In this paper, I outline some recent developments in the application of evolutionary theory to human demography. Rather than reviewing the entire field, which is very large, I will illustrate this approach by tackling what might be considered the most challenging question raised in the discipline: namely, what is the evolutionary basis for the failure of some people to reproduce? A simplistic analysis might suggest that humans (and indeed any species) should, subject to constraints, be evolved try to reproduce at the maximum possible rate. I will examine how evolutionary demographers and biologists have explained three contexts in which humans either do not reproduce, or do so far less than is theoretically possible: homosexuality, menopause, and the demographic transition. I will conclude by responding to some of the theoretical issues the other contributors to this volume are also addressing.

Biologists generally define evolutionary demography as the application of life history theory to population processes. Having worked in both the biological and the social sciences, I often switch between the two different vocabularies of the social and biological sciences. One difference between these scientific disciplines is that the phenomenon that demographers call fertility (the number of births, which is the definition I use), biologists call fecundity. The two fields are similar in many respects. Life history theory is a well-developed sub-discipline of evolutionary ecology which is explicitly concerned with the timing of life history events (growth, reproduction, maintenance, and death) under natural selection. The timing and the scheduling of births in order to maximise fitness (in the Darwinian sense) can in theory be calculated for any given environment and any given set of environmental constraints. In examining the timing of births, researchers often try to understand both the behavioural and the physiological determinants of fertility (e.g., menopause). Parental investment is viewed as a life history trait that is determined in part by considerations regarding the quantity versus the "quality" of offspring. It has long been recognised that maximising reproductive success is not necessarily about maximising fertility alone. A "Darwinian demon" who reproduces at the maximum rate would not succeed in the real world, as

there would be costs of reproduction for the mother (and probably even for the father), and there would be competition between siblings for parental resources. Trading off these costs with the fitness benefits of fertility ultimately determines the rate and nature of human reproductive decisions.

At this point, it may be useful to clarify the meanings of certain terms that are often used differently in different disciplines, and especially to explain what evolutionary biologists mean when they refer to "ultimate" explanations. Evolutionary biologists describe the environmental cues used in reproductive decision-making, or the physiological condition that an organism achieves that influences its fertility, as "proximate" determinants of fertility. This definition of proximate determinants of fertility is similar to – although perhaps more general than – the sense in which Bongaarts famously used the term (Bongaarts, Frank, and Lesthaeghe 1984). Evolutionary biologists refer to the reason why a particular behaviour maximises Darwinian fitness as its "ultimate" function (Krebs and Davies 1984). Biologists often use the term reproductive "decision-making" to refer to the costs and benefits that shape reproduction, even if active decision-making in the usual sense of cognitive deliberation does not really apply (for example, the term is often used in studies of birds, bats, and many other species, however small their brains). Evolutionary demographers are interested in both proximate (mechanistic) and ultimate (evolutionary) explanations. It is important to emphasise that these two explanations are related, not contradictory. For example, the extent to which a specific behaviour is genetically heritable has no real bearing on its function. Many cultural behaviours – such as teeth-cleaning or not having children unless a union is sanctioned by marriage – may improve an individual's reproductive success without having any genetic basis. The environments in which these behaviours are beneficial may therefore depend on the cultural context. But humans are smart, and can learn on their own or be taught by their cultural parents to apply these "rules" only when these prescripts enhance fitness in a given context. We may have genetic predispositions to, for example, have sex, have children, secure plenty of food, and avoid dangers to our lives or our children's lives. But cultural rules can still guide us in determining how to best fulfil those desires in a particular society by sanctioning certain behaviours.

As social and societal contexts influence the costs and benefits of various behaviours, these contexts are integral to any evolutionary ecological model. Evolutionary models tend to interpret behaviour in terms of the costs and benefits to the individual, while assuming that societal factors influence those individual costs and benefits, or the knowledge of them (i.e., the social world is treated as part of the relevant environment). However, some models (in both evolutionary biology and evolutionary anthropology) also acknowledge that the benefits (or the costs) to the

individual can operate through the success or the failure of the group in which the person lives (Frank 1995; Richerson and Boyd 2005).

Mathematical simulations have been used to predict that cultural rules that are maladaptive (in the sense that they do not obviously benefit the inclusive fitness – that is, the direct and indirect fitness – of individuals and their kin) rarely become established in populations. This is because evolutionary processes are acting on both genes and on cultural traits. Theoretically, given that cultural inheritance mechanisms are not the same as genetic inheritance mechanisms, we may assume that cultural traits that have been successfully transmitted from one person to another could, at least in the short term, become features of a society, even if they do not promote genetic fitness. There are significant disagreements in the literature about the extent to which maladaptive cultural behaviours persist over the long term in populations. Understanding human fertility is one arena in which this debate continues. Arguments about how cultural evolution differs (or does not differ) from genetic evolution is an issue I will return to below. The extent to which individuals might copy other individuals or be influenced by the choices of those around them, rather than trying to work out costs and benefits based on their own experience, is still not well understood.

If any aspect of a society – or indeed any aspect of a person's environment – has recently changed in ways that would not have been possible in previous human evolutionary history, then evolutionary models may be unable to predict observed behaviour, as natural selection takes time to work. This problem is sometimes referred to as mismatch or evolutionary lag. The question of how quickly individuals respond to changing cues has not yet been sufficiently explored, but this gap in our knowledge is perhaps more a failure of empirical research than of theory.

While evolutionary theoretical approaches should in theory have the unique ability to predict how behaviour will vary with environmental conditions, applying evolutionary models in modern contexts has been difficult in practice. If many aspects of contemporary environments are novel (in evolutionary terms), it is hard to predict how humans will respond. Attention to proximate mechanisms, including learning, becomes very important in anticipating behaviour. The extent to which individuals might copy other individuals or be influenced by the choices of the people around them is a question that has so far been addressed by only a small number of researchers. As most social scientists are concerned with proximate mechanisms (rather than with the ultimate evolutionary function), empirical work in a range of disciplines could prove relevant in this field of enquiry. An evolutionary approach could provide a clear theoretical framework that would allow researchers to predict which proximate mechanisms are important, and thus has the potential to drive the field forward.

2. Previous and current work in evolutionary demography

Evolutionary demography has made fundamental contributions to our understanding of reproductive scheduling (both physiology and decision-making), and has also generated many practical findings. The idea that parental investment is linked to mating strategies, mortality risks, and all other life history traits was not well understood prior to evolutionary analyses of these issues. The results of studies in this field have also been of considerable practical significance. Some of the most important work that has been done in evolutionary demography is in the area of child abuse and child homicide, including a study which highlighted the role of unrelated new partners of mothers in child abuse or neglect (Daly and Wilson 1988). Following the publication of this study, the results were replicated in different settings all over the world. While these findings have clear policy implications, they have not always received adequate attention from policy-makers (Daly and Perry 2011). The insight that unrelated father figures are likely to cause more stress and conflict than genetic fathers has been shown to apply even in cases in which no abuse is involved. Accidental child deaths with no criminal intent (such as accidental drowning in swimming pools) have been shown to be more common when the mother is in a new relationship, which suggests that the effort a mother might normally put into parental care could be diverted towards her new relationship (Tooley et al. 2006). In a cohort of randomly selected UK children, we have shown that relative to the stature of children in families in which the father is present, there is a small reduction in stature among children in families with an absent father, and there is a still small but more significant reduction in stature among children in families with an unrelated co-resident father figure, especially among boys (Figure 1, results from Lawson and Mace 2008). These findings illustrate the potential fitness costs to fathers that men must weigh against the potential benefits when they consider leaving one family to start another. The desire for the successful production and rearing of genetic offspring underpins our reproductive decision-making, regardless of whether those decisions are related to mate choice, fertility, or parental investment (all of which are, of course, strongly interlinked).

Figure 1: **Height difference in mm in children aged 10 with either father absent (black bars) or step-father present (grey bars), relative to height of 10-year-olds who live with both genetic parents (father present), for a) boys and b) girls**
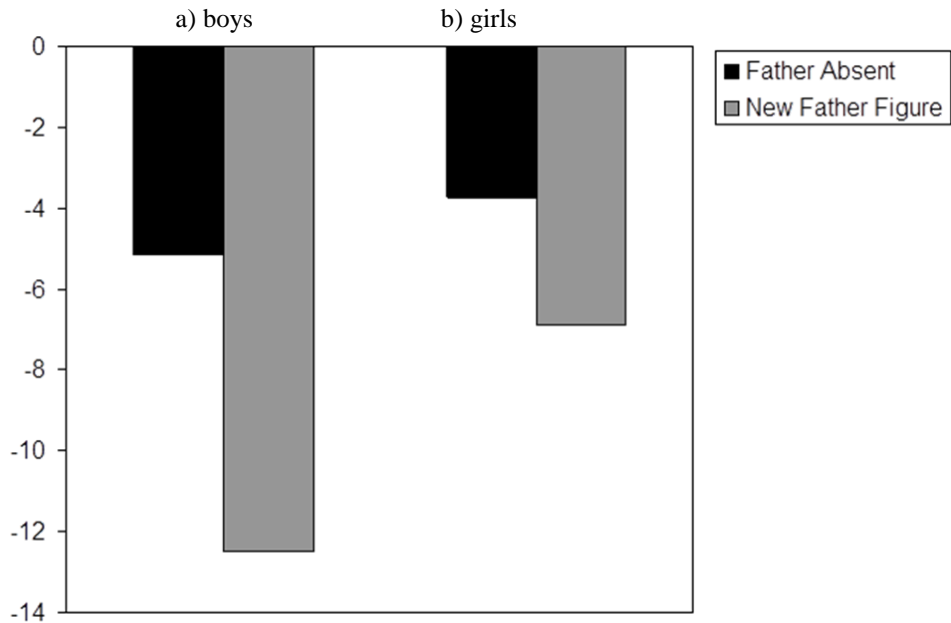
Source: Lawson and Mace 2008.
Notes: Reduced stature indicates stress during childhood growth, and new father figures appear to be more stressful for boys, and to be more stressful than simple father absence.

Clearly the desire to have children is not hard to explain in evolutionary terms – maximising Darwinian fitness is our *raison d'être*. Evolutionary reasons not to have children are therefore more interesting to an evolutionary demographer. The conundrum of phenomena that appear to curtail human fertility has stimulated a rash of research on questions such as the following: why does fertility decline in populations experiencing economic development (the demographic transition), and why does fertility decline in later life, and especially rapidly for females (menopause)? I will discuss both of these issues in greater detail below, not because they are the only questions that evolutionary demography is in the process of addressing, but because they happen to be among my own subjects of research. Voluntary childlessness and homosexuality are other examples of apparently maladaptive behaviours that have received relatively little attention from evolutionary ecologists. In any single individual, childlessness could to

be related to failures in mate choice. But ultimately any behaviour associated with reduced fertility that is not due to constraints and is a stable feature of human behaviour in a given environment – rather than being a short-term maladaptive behaviour that will only persist long enough for evolution to correct it – can only be explained as an adaptation in evolutionary terms if it is related to indirect benefits to kin or existing children. Below I will explain how this process might operate in three particular cases.

Recent research on determinants of reproductive scheduling has examined the question of how people decide when not to have a baby.I will discuss three potential contributors to low fertility which differ from each other, but which appear to be important in evolutionary terms: 1) homosexuality, 2) menopause or late-life low fertility, and 2) the demographic transition to low fertility. I addressed two of these topics in a review in 2000 (Mace 2000), and continue to be interested in these issues as new discoveries about them are being made with new models and new data. In all three cases I will argue that it is possible to explain these potential sources of low fertility by examining reproductive competition within families.

1)   How can male homosexual preference evolve by natural selection?

Male homosexual preference (MHP) is too common to be understood as a trait that natural selection has ignored. While it is not seen as a persistent trait in wild animals, it is occasionally documented in anthropological studies of hunter-gatherers. Hill and Hurtado described a "homosexual" phenotype that is rare among hunter-gatherers, but has been observed among the Ache people. According to their accounts, some Ache men displayed effeminate behaviour and did not reproduce, but they did not engage in homosexual sex until after they were exposed to Paraguayans (Hill and Hurtado 1996). Many traditional societies recognise more than two genders. As the homosexual phenotype appears to be common across the globe (2%–6% in western societies), researchers assume that it must have been subject to natural selection. While there is little evidence that homosexual brothers are of direct benefit to their kin (Bobrow and Bailey 2001; Vasey, Pocock, and VanderLaan 2007), scholars have speculated that they may be of indirect benefit by, for example, reducing competition between the other siblings for parental resources. There is evidence that male homosexuality shows a clear birth order effect, with each elder brother (but not sister) significantly increasing the likelihood of homosexuality in males (Blanchard 2001). It has also been suggested that sisters of homosexuals may be more fertile than women who do not have homosexual brothers (Camperio-Ciani et al. 2004). This could be due to shared genetic effects such as feminine beauty (which is advantageous to fertility in females but has disadvantageous pleiotropic effects in males); or it may simply be a side effect of large families being heritable, as large families are associated with both a higher level of

female fertility and a higher incidence of male homosexuality in younger brothers. Michel Raymond and colleagues have built a model for the evolution of male homosexual preference which shows that, in a stratified society, a relatively high frequency of MHP could be maintained as a result of the social ascension (or up-migration through social strata) of females signalling high fertility (hypergyny) (Barthes, Godelle, and Raymond 2013). Their prediction that MHP is more prevalent in stratified societies was significantly supported in a sample of 48 societies for which the presence or absence of MHP was anthropologically documented. They argued that any traits associated with up-migration are likely to be selected for in a stratified society, and will be maintained by frequency dependence even if they induce a pleiotropic cost, such as MHP. These results offer new perspectives for understanding seemingly paradoxical traits in human populations.

2) *Is menopause an adaptation to co-operation or to conflict?*

Grandmothering might be selected for because grandmothers have historically been co-operative breeders and they help their daughters reproduce (Hawkes et al. 1998). This hypothesis stimulated a sharp increase in interest in kin effects on human fertility, and provides an example of how evolutionary demography has helped to set the agenda beyond the evolutionary field. In co-operative breeding some individuals give up reproductive success to help others (kin) reproduce, whereas in communal breeding several females rear offspring together. Humans are less likely to engage in communal breeding, in part because menopause lessens the likelihood that female kin of reproductive age will reside in the same household; although in some matrilineal societies, such as the Mosuo of south-western China, sisters do co-reside and breed communally (Wu et al. 2013). Studies of co-operative and communal breeding in animals have focused much more strongly on reproductive conflict between individuals (Clutton-Brock et al. 2010); whereas human studies have tended to focus more on the co-operative benefits of communal life and its relevance for the evolution of menopause (Hawkes et al. 1998), albeit with some exceptions (Ji et al. 2013; Strassmann 2011). Human life history is characterised by a long childhood, followed by a rapid reproductive phase, and then a long post-reproductive life, at least for females. It has been argued, with some speculation on this topic going back to Williams (1957) and (Hamilton 1966), that human menopause might be selected for by kin selection favouring older mothers investing in their grandchildren rather than continuing to reproduce themselves (Hawkes et al. 1998). There is now considerable evidence that grandmothers enhance the reproductive success of their offspring (reviewed in (Sear and Mace 2008)), including findings from our own study in rural Gambia (Mace 2000; Sear, Mace, and McGregor 2000; Sear, Mace, and McGregor 2003). The evidence is

especially clear that the presence of a maternal grandmother facilitates grandchild survival across a wide range of societies, although kinship norms may influence which residence patterns are the most favourable (Leonetti and Nath 2009). Predictions derived from life history models do not agree on the question of whether the grandmother effect alone could select for menopause to be favoured by natural selection. Some scholars have argued that the effect of mothers on offspring is more important (Peccei 2001), or that it is post-reproductive life that has evolved as the derived trait, with fertility constrained at around age 50 (Hawkes et al. 1998). These are, however, verbal models. Mathematically the results of these models are more similar than they may appear, as in order to demonstrate that menopause is the subject of selection, the models need to show some benefit of a separation of reproductive ageing from somatic ageing. Some mathematical models informed by data failed to predict any fitness benefit associated with terminating reproduction so long before death (Hill and Hurtado 1996), or they found that any benefits that do exist are rather marginal (Shanley et al. 2007). More research on this issue is therefore needed.

Implicit in all the various models of the grandmother hypothesis is the notion that mothers and daughters are in reproductive competition, as it is assumed that only by becoming non-reproductive can a grandmother really support her daughter's reproduction. It is striking in humans how little human female generations overlap (Figure 2): as a daughter reaches reproductive age, her mother reaches menopause; and as the daughter reaches menopause, her mother dies. However, while reproductive conflict predicts that reproductive generations should reduce overlap, it not does address the question of why the older woman rather than the younger woman foregoes reproduction, as is generally the case in most co-operatively breeding birds or mammals (Clutton-Brock et al. 2010; Hatchwell and Komdeur 2000). Johnstone and Cant argued that this competition is particularly intense for older females in species in which females disperse, as this means that the older females will not be closely related to the younger breeding females entering their group (Cant and Johnstone 2008; Johnstone and Cant 2010). Female dispersal is unusual among mammals, but is thought to be the most common arrangement among chimpanzees (*Pan troglodytes*) and possibly among ancestral humans, although there is variation in the residence patterns of contemporary hunter-gatherers (Hill et al. 2011). Johnstone and Cant have modelled a scenario in which females compete for resources for reproduction within their groups. Under patrilocal residence (that is, when females disperse at breeding ages and males do not disperse), the relatedness of an adult female to the group will be low at the point of her arrival in the new group, and the other females in the group will normally be only distantly related to her, if at all. Relatedness to the co-resident group will gradually increase with age as the woman's own offspring (particularly sons who do not disperse) are born and then grow up to reproduce themselves. We have shown that this pattern in

relatedness to co-residents applies in the case of patrilocal compounds (where fathers, sons, and brothers, together their families, co-reside) in rural Gambia (Mace and Alvergne 2012). When an older woman finds herself in competition with her son's wife for reproductive resources, there is an essential asymmetry in that the older woman is related to her son's offspring (and will thus suffer a fitness cost if she harms the reproduction of her son's wife); but as the son's wife is not related to the older woman's offspring, natural selection does not favour her helping her husband's mother to reproduce. The ESS models show that the younger woman is more likely to win the competition, and the older woman is destined to become the sterile helper. Johnstone and Cant (2010) argued that this helps explain late-life low fertility in whale and primate groups in which females either disperse or mate outside the group, and that humans generally fall into the former category. This raises the possibility that part—and perhaps the greater part of a grandmother's contribution is her failure to compete, and that this is linked to sex-biased dispersal patterns. This argument is interesting, as it appears to contradict previous hypotheses which asserted that grandmothers should play a bigger role in matrilocal than in patrilocal societies because maternal grandmothers appear to be the most helpful.

Reproductive conflict generally leads to attempts by dominant breeders to control less dominant ones, and it may well be in the genetic interest of less dominant individuals to help more powerful kin reproduce rather than to pay the costs of trying to compete with them to reproduce (Emlen 1995; Ji et al. 2013; Ji, Xu, and Mace 2014). Human parents are usually in quite a strong position when it comes to controlling offspring reproduction through the timing of marriage, especially if parental wealth is heritable and is needed to facilitate marriage (Mace 1996). In such cases, offspring cannot easily marry without parental consent. In the Gambian community we studied, men need access to fields in order to farm and to a bride-price in order to marry. To obtain these resources, thee men usually require the co-operation of their patriline. Traditionally, the first marriages of all children are arranged by the parents, especially the father. After marriage it is less likely that parents or other kin would be able to exert much control or influence over the rate of birth ((Mace and Colleran 2009), but our earlier findings suggested that paternal grandmothers may increase fertility in their sons' wives (Sear, Mace, and McGregor 2003)). Therefore, the issue of reproductive conflict within two generations of the same family is avoided partly by cultural rules that dictate when marriage occurs, and partly by the biological reality of menopause. In historical Finns, the very few instances of co-residence of reproductive mother-in-law/daughter-in-law was associated with reduced fertility (Lahdenperä et al. 2012). But if parents can control their son's reproductive opportunities by delaying has marriage, they can reduce intergenerational reproductive conflict. In the Gambia, the cultural norm of late male marriage reduces the overlap in the reproductive spans of mothers

and daughters-in-law almost to zero (Figure 2, Mace and Alvergne 2012). However, daughters are often allowed to marry prior to the end of their mothers' reproductive lives, although we have shown previously that an early age at the first birth is associated with a prevalence of male kin (especially brothers) in the natal household (Allal et al. 2004). A family's need to acquire brides for male kin, and thus to accumulate the resources to pay the bride-price, may therefore influence the decision of when the daughters marry. Furthermore, there is a reluctance to delay marrying off daughters as they may become less marriageable with age. The reproductive stage of a girl's mother is therefore unlikely to be the only consideration in the timing of her marriage, and could lead to some instances of potential reproductive competition. Because daughters move out of the natal household at marriage or shortly after the first birth, intergenerational competition between female kin for household resources is thus reduced. This social arrangement is known as patrilocality or virilocality. It may therefore be the case that kinship, residence, and marriage norms in human societies are themselves cultural adaptations for reducing reproductive conflict in human groups (Ji, Xu, and Mace 2014; Mace and Alvergne 2012). Fertility schedules and rates could be co-evolving with human kinship systems, with an earlier female age at the first birth (and possibly a later male age at the first birth) associated with patrilocal residence. However, it should be noted that patrilocal residence means fathers and sons co-reside, and fathers are normally more dominant than sons; if male competition is more important than female competition in determining who wins in the reproductive conflict, then the exact opposite is predicted and patrilocal residence would not necessarily be associated with menopause (Ji, Xu, and Mace 2014).

Figure 2: **Age at time of birth for mothers, maternal grandmothers, and paternal grandmothers in rural Gambia**
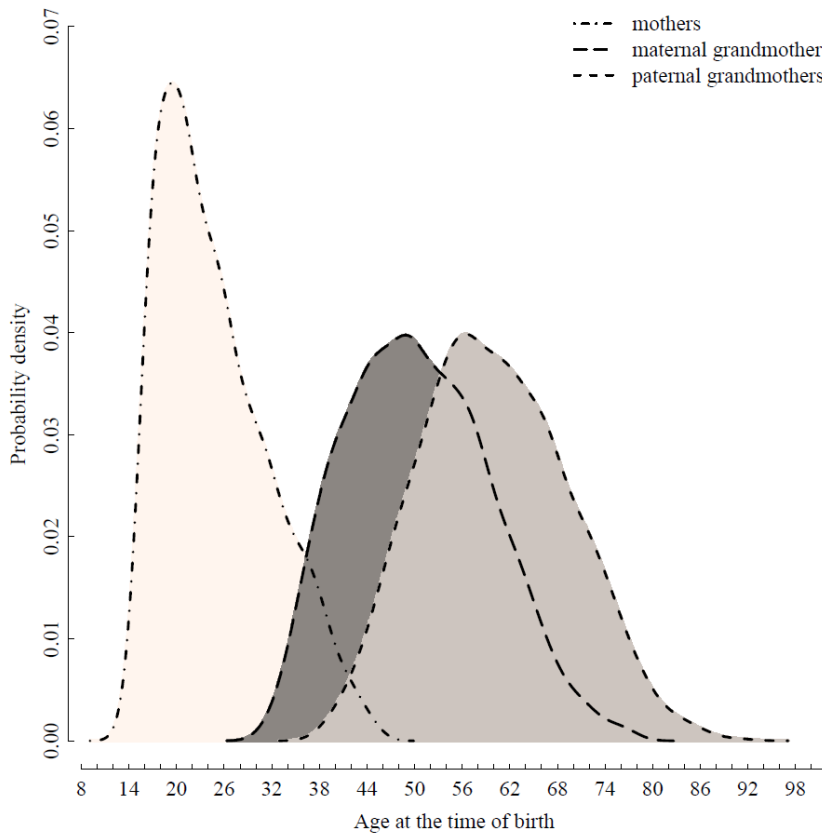
Source: Mace and Alvergne 2012

3) *The demographic transition to low fertility: Is it caused by cultural influences or changes in costs and benefits?*

The classic concern of demographers with the decrease in fertility that accompanies the decline in mortality and industrial development in a society has also long been of interest to evolutionary demographers, who are fascinated by the perplexing question of why an increase in wealth would lead to a decrease in fertility. This issue has also been the subject of some empirical if not theoretical investigations over the past decade.

Explanations in evolutionary demography, like those in general demography, have tended to fall into two categories: those related to the costs of children and those related to the cultural transmission of new ideals about low fertility.

Evolutionary demographers who favour the hypothesis that costs and benefits drive the decline in fertility have consistently focused on the costs of high parental investment. Children are less useful as labourers now that fewer people are farmers and children need to spend more time at school. The opportunity costs of reproduction are also rising as education is becoming an important part of future earning capacity. Kaplan and others have argued that, as the trade-off between education and reproduction shifts towards education, women reproduce later. In some cases, women may overestimate the benefits of education (in evolutionary terms) and have fewer offspring than they want, or even wait too long to try to get pregnant (Kaplan et al. 2002). It is also reasonably clear that parental investment might be co-evolving with wealth inheritance, which would limit fertility (Mace 1998). Moreover, the parental investment process may be snowballing, driven by competition between individuals who favour "quality" over quantity in offspring (Hill and Reeve 2005; Mace 2008). This could make competition between siblings for parental investment more, not less intense in modern societies. Some scholars have expressed scepticism about whether competition is important in modern families in which mortality is very low. While it is still not very easy to determine in modern societies how important sibling competition for parental investment is in fitness terms, we now have more evidence that sibling competition for parental investment is real. (Lawson and Mace 2010) examined a large cohort of UK children, and found that the presence of siblings is associated with very significant reductions in time spent on parental care. The study showed that even in a country with free education and health care, children with many siblings are shorter in stature, have worse results in their exams, and receive much less care from their parents (at least in terms of time spent caring). Furthermore, there is some evidence that this competition is actually more, not less intense in wealthier households and in wealthy societies (Lawson and Mace 2011). It is possible that historical norms that allowed for discrimination between offspring (in terms of inheritance or other investments) enabled parents to cope more easily with large families: i.e., those children who did not inherit had to make their own way in new businesses or institutions, such as the army or the church, leaving the farm or other household resources undivided for the use of one inheriting offspring. Whether these effects are large enough to drive fitness differences, or whether the systems that generate low fertility have been around long enough for selection to have made these responses adaptive in the evolutionary sense, are questions to be addressed in future research. However, the evolutionary framework has at least helped to identify the kind of proximate effects that might be leading to reduced fertility in modern families. If competition is intense, then mating strategies may reflect this

competition: i.e., individuals will maintain high standards when looking for a mate, and may even risk not finding a suitable mate at all and remaining childlessness. A combination of modelling and data analysis will be needed to explore this hypothesis further.

Cultural evolutionary models have raised the possibility that low fertility could be the result of "prestige biased copying" (Boyd and Richerson 1985). More generally, models of "cultural group selection" suggest that either conformity or punishment, or a combination of the two, could lead to behaviour that benefits the group, which may include limiting fertility. However, just as in the mainstream demographic literature demographers are debating the role of diffusion in the demographic transition, there is a debate among evolutionary anthropologists and biologists about the extent to which cultural transmission is causing the fertility decline. In our study in rural Ethiopia, we found little evidence that the decision to start using contraception was influenced by friends or family in the immediate proximity or in the immediate social network, although religious affiliation was found to have an effect (Alvergne et al. 2011), as has also been shown in Bangladesh (Munshi and Myaux 2006). It may, for example, be the case that cultural transmission occurs only within religious groups. But it is also possible that religious institutions impose different costs on individuals, and that the effect of religious affiliation is itself an individual response to costs and benefits. Meanwhile, land inheritance has been shown to predict contraceptive use in Ethiopia, as individuals with private landholdings to pass on were found to be more likely to use contraception (Gibson and Gurmu 2011), in line with the predictions of behavioural ecological models (Mace 1998). Shenk et al. also tested the relative importance of both cost/benefit variables and cultural transmission variables as correlates of low fertility within the same population in Bangladesh. They found that heritable wealth was an important factor in contraceptive use, and that the role of cultural transmission was not significant (Shenk et al. 2013). However, they used fairly loose correlates of cultural transmission (such as listening to the radio) rather than examining the substructure of the population to identify the presence of clustering, social networks, or other potential determinants of cultural transmission. Thus, the issue is not yet fully resolved, and it may be the case that both costs and benefits and cultural transmission contribute to low fertility (Mace 2013). While education clearly plays a central role in the fertility decline, the effect of education may operate in part through its ability to influence the patterns of cultural transmission between individuals (Borenstein, Kendal, and Feldman 2006). In a study of 22 villages in rural Poland where the demographic transition is underway, Colleran et al. found that fertility is just as associated with education at the village level as with the socioeconomic position at the individual level; and thus provided some support for this view (Colleran et al. 2014). Cultural influence could matter more for neutral traits (such as the decision about whether use a particular type

of contraceptive) or for relatively trivial traits (such as fashions) than for matters that profoundly influence reproductive success (such as the decision about whether to use any type of contraceptive at all).

I have not attempted to cover all aspects of evolutionary demography in this short paper, but have instead chosen to highlight some of the recent work in the field that addresses conundrums regarding low and declining fertility. All the adaptive explanations for phenomena associated with low fertility posit that reduced fertility provides some indirect benefits to kin. My wider intention here is to suggest that while the subjects of interest in evolutionary studies of fertility are in many cases similar to those of interest in other disciplines, evolutionary demographers and anthropologists have developed some new hypotheses and new variants of old hypotheses that may prove useful in investigations of low fertility. In addition, these scholars have strong backgrounds in hypothesis-testing in the field, and wield a new tool kit of investigatory measures and methods that can help to inform the study of low fertility.

3. A summary of approaches to key questions

1) *How does the theory explain the kind and amount of parental investment in children?*

Parental investment is assumed to be an adaptation to maximise the long-term reproductive success of parents. It is generally considered as a life history variable along with the timing of reproductive events, and it might be seen as an investment in the growth and development of offspring. Thus, both the timing and the spacing of births is related to parental investment, which is in turn ultimately related to the long-term prospects and mortality risk of the children. Life history theory predicts that in all species, high extrinsic mortality rates tend to lead to a "faster" life history, in which children are born earlier in the life of the mother and at shorter intervals. This is because even though early and frequent childbearing is associated with additional mortality risk, a strategy of high investment in individual offspring does not pay off if there is a good chance that extrinsic factors (i.e., factors over which parents have little control), will cause the death of the child before he or she can reproduce. Wealth, care, and education can all be considered and investigated as forms of parental investment, and the tools of evolutionary ecology and life history theory can be used to understand their variations. Interestingly, this theory has also proven to be a valuable framework for explaining some aspects of child mortality or low levels of parental investment, as it is the reproductive success of the parents (which is sometimes in conflict with the reproductive success of the children) that is being maximised. In environments in which

mortality is high, very high levels of fertility might be associated with high levels of infant mortality, but they nonetheless maximise a mother's lifetime reproductive success (for example, in rural Gambia mothers with twins often had high levels of child mortality but more lifetime reproductive success than those without twins (Sear et al. 2001)). Evolutionary processes generate physiologies and behaviours that maximise Darwinian fitness, not happiness.

2) *In what ways does the theory consider the social and the societal contexts of fertility, and which dimensions or levels of the contexts of individual fertility are addressed in particular?*

Evolutionary ecological models predict how a behaviour will maximise reproductive success in a given environment. In that sense the context of the behaviour, including the social and the societal contexts, will be key elements of any evolutionary ecological model. The strength of the approach lies its ability to predict how behaviour will vary in different ecological or social contexts.

3) *What is the unique contribution of the theory to the explanation of fertility in developed countries? How does it differ from or contradict other theories? In what ways is it complemented by other theories?*

Evolutionary theory is unique in terms of providing a theory for all life, be it physiology, development, or behaviour. The maximand of evolutionary models is Darwinian fitness, or reproductive success. The evolutionary approach shares many ideas with economics, as it investigates how costs and benefits drive behavioural variation. But evolutionary models also differ from economics in that in evolutionary models the currency of "utility" is Darwinian fitness, whereas in economic models it can be anything identified as a preference. An economic model is only evolutionary if that preference can be explained as benefitting the fitness of the individual, or could reasonably be assumed to benefit fitness if people were living in an environment in which the behaviour evolved. If our current societal conditions emerged very recently in response to industrialisation and urbanisation, evolutionary demography may not be able to predict current behaviour. Furthermore, as child mortality was probably the most important selection pressure acting on reproductive decision-making, it is not clear how much selection there currently is on human fertility behaviour now that both child mortality and fertility are low. However, even in modern settings having an uncertain future and a higher mortality risk are factors that are still associated with earlier childbearing (Wilson and Daly 1997). As levels of childlessness are now quite high in

some contemporary human populations, it seems likely that selection for factors that avoid childlessness must continue to be high.

Many studies have looked at measures of cultural success such as educational achievements or wealth as proxies for reproductive success, although the degree to which these indicators map onto reproductive success is not consistent. However, gaining a better understanding of our evolutionary history and of what elements of our physical and social environment have and have not changed will help us hone the effectiveness of our approaches. Evolutionary theory has much to say about mate choice, parental investment, and sibling competition – factors which influence not just behaviour in traditional small-scale societies, but also behaviour in developed societies.

Evolutionary demography has benefited greatly from the statistical and analytical advances made in demography. The trend towards looking at individual variation rather than just population measures has brought non-evolutionary and evolutionary demography closer. There are numerous areas of common interest between demography and evolutionary life history theory. Cultural evolutionary models also now touch on many areas of wider interest to demographers, such as the importance of diffusion and social learning in changing cultural norms of fertility.

4)   What is missing in extant theories of fertility behaviour?

It is still the case that the evolutionary framework is more successful at predicting behaviour in traditional societies. Nonetheless, the lack of fit with models of modern systems is more quantitative than qualitative. Gaining a better understanding of the impact of rapid cultural change on behaviour in general and fertility in particular would be useful. To what extent the behaviour of those around us influences our own behaviour is a question that has not yet been adequately studied.

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