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Wealth, fertility, and adaptive behaviour in industrial populations

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ABSTRACT

The lack of association between wealth and fertility in contemporary industrialised populations has often been used to question the value of an evolutionary perspective on human behaviour. Here, we first present the history of this debate, and the evolutionary explanations for why wealth and fertility (the number of children) are decoupled in modern industrial settings. We suggest that the nature of the relationship between wealth and fertility remains an open question because of the multi-faceted nature of wealth, and because existing cross-sectional studies are ambiguous with respect to how material wealth and fertility are linked. A literature review of longitudinal studies on wealth and fertility shows that the majority of these report positive effects of wealth, although levels of fertility seem to fall below those that would maximise fitness. We emphasise that reproductive decision-making reflects a complex interplay between individual and societal factors that resists simple evolutionary interpretation, and highlight the role of economic insecurity in fertility decisions. We conclude by discussing whether the wealth-fertility relationship can inform us about the adaptiveness of modern fertility behaviour, and argue against simplistic claims regarding maladaptive behaviour in humans.

1. INTRODUCTION

In an update to Jane Austen's famous pronouncement of "a truth universally acknowledged, that a single man in possession of a good fortune must be in want of a wife" ([1], p. 1), Vining suggested that, in contemporary society, it was a negative relationship between wealth and fertility (the number of children) that was close to "a universal regularity" ([2], p. 168). Pérusse [3] argued similarly that wealth and fertility were decoupled in industrial societies, given that wealthier men did not father more offspring despite higher mating success. These papers have been said to characterise the "central theoretical problem of sociobiology": if, as evolutionary theory assumes, individuals are attempting to maximise their fitness, more resources should translate into a larger number of offspring, as seen in a range of pre-industrial populations (see e.g., [3–9]). The lack of a positive relationship between resources and reproductive success also fits with the large-scale pattern of fertility decline in recent history, whereby fewer children are born in more prosperous economies (e.g., [10]); whatever people are doing with the resources they acquire so assiduously, they are not, apparently, investing them in having more children.

Here, we revisit briefly Vining [2] and Pérusse [3], using them as springboard for a survey of the literature on wealth and fertility among industrial populations (see also [11]). We present a new review focused exclusively on longitudinal studies that enables stronger inferences to be made about the links between wealth and reproduction. Finally, we discuss the extent to which the association between wealth and fertility speaks to the issue of (mal)adaptive behaviour, and argue for a more biosocial approach to human fertility.

1.1. Vining & Pérusse: strong conclusions, weak foundations

Despite receiving frequent citations to this day [12], both Vining's and Pérusse's papers met with strong resistance at the time of publication—something that is immediately apparent in the commentaries accompanying each article. In Vining's case [2], the negative or null relationships he claimed to have established were called into question by, among other things, the use of unrepresentative convenience samples, fuzzy notions of social success and status that attempted to capture access to "superior resources"(p. 168; i.e., the use of proxies as diverse as material wealth, occupational status, "eminence", and intelligence), and the inclusion of people who had not yet completed their reproductive careers. Moreover, a number of the relationships Vining found were actually positive; something that did not, however, lead him to doubt his "universal regularity". In Pérusse's case, similar criticism was directed at the snow-ball sampling design using Quebecois college students, the composite measure of different status markers, some rather simplistic analyses (e.g., Bookstein went so far as to call these a "polemical abuse of statistics"; [3]; p. 286), and some very small sample sizes. Pérusse also makes the assumption that, in a world without contraception, wealthy men would have achieved the same number of additional matings as they do today, and that these would translate into higher fertility; in his view, widespread contraception creates a mismatch between our past and present environments and disrupts the wealth-fertility link.

1.2. The response from Human Behavioural Ecologists

Despite their flaws, there was a period following the publication of Vining's and Pérusse's papers when Human Behavioural Ecologists seemed willing to entertain the idea that wealth was not positively related to fertility in Western society (fuelled also by work in economics, where the relationship had been explored since the 1960s, most notably by Becker [13]). A good deal of effort was thus devoted to generating evolutionarily-oriented explanations for why resources might not be channelled into offspring, and why fertility within industrialised nations should be so low (see e.g., [14] for an early review). These responses came in two flavours: 1) theoretical and formal mathematical analyses exploring the conditions under which it would be adaptive to limit fertility and why the wealthy, in particular, should do so; and 2) novel empirical studies of the wealth-fertility relationship.

2. THEORETICAL TREATMENTS OF WEALTH AND FERTILITY

A number of theoretical studies have focused on the idea of a mismatch between ancestral and modern environments, suggesting that modern reproductive strategies are not fitness-enhancing. Draper [15] and Turke [16], for example, argued that, in pre-industrial populations, the costs of raising a child, in terms of both time and resources, are dispersed throughout extended kinship-networks whereas, in industrial settings, they fall on the nuclear family alone because of reduced interactions with kin (see [17,18] for similar reasoning). Material wealth may therefore be "a less than perfect substitute" for familial support when it comes to fertility outcomes ([16]; p. 68).

In addition, it was suggested that humans may be psychologically predisposed to attune decisions to those occurring in their "reference groups" ([19]; e,g, those of similar occupational status or education; see also [20,21] for perspectives from economics). That is, people are argued to attend to, interact and compete with a specific subset of the population, which leads to biased perceptions of wealth and the actual cost of raising children. Alternatively, people may be predisposed to copy the behaviour of other reference groups, specifically those high in prestige [22], which may result in limiting fertility under the (perhaps mistaken) assumption that such behaviour leads to better outcomes. Others have argued that, because children face intense competition with peers to get ahead and there is no real limit on parental investment (i.e., children will always be of higher quality if they receive continued heavy investment), "run-away" processes are likely, which favour high expenditure on offspring and, because resources are finite, result in low fertility [23,24].

Another set of analyses considered whether limiting fertility could, in fact, maximise long-term fitness. Several formal theoretical treatments confirmed that reducing fertility could be adaptive under certain conditions ([25–27], but see [28]). However, there were no conditions under which the wealthy were expected to lower their fertility more than their poorer counterparts. Models designed to address this latter point explicitly suggested that foregoing higher fertility either to invest in higher social status (so decreasing the risk of mortality during very harsh periods [29]) or to enable intense investment in wealth accumulation for descendant lineages [24], could increase long-term fitness by reducing the likelihood of lineage extinction (see also [30]).

2.1. Embodied-capital theory and the economics of fertility

The most comprehensive and influential examination of the breakdown of the relationship between resources and fertility, and the rise of very small family size, is Kaplan's embodied capital theory [31]. This explicitly combines Gary Becker's influential economic theory of fertility (e.g., [13,32]) with life history theory (LHT; e.g., [33]), and incorporates an evolutionary psychological mechanism to explain why wealth and fertility have become decoupled across human evolutionary history. In line with classical LHT, the theory assumes that there will be particular trade-offs between investments in growth, maintenance and reproduction that natural selection will favour; for instance, a trade-off between offspring quantity and quality (e.g., [34,35]; one that is also highlighted in the economic literature: [32]).

According to Kaplan [31,36], human fertility regulation mechanisms are adapted to the selection pressures of the learning-dependent, skill-intensive hunter-gatherer foraging niche (see [37] in this issue for a more elaborate account of Kaplan's theory). Given that "wealth" in the ancestral state is comprised of food energy alone, the accumulation of "embodied capital" under these conditions automatically translates into offspring via female reproductive physiology. Under these conditions, a model of embodied capital maximises fitness [36]. When applied to non-hunter-gatherer societies, however, there is no guarantee that high levels of embodied capital will translate into high fertility for the following reasons:

First, our fitness-enhancing preference for resources are argued to be distorted by the existence of new extra-somatic forms of wealth (livestock, land, money), which, unlike food resources, are not automatically converted into offspring, and may be accumulated for their own sake. Extra-somatic wealth seems to be consistently related to higher fertility in a number of pastoral and agricultural societies (e.g., [3–9]), however, so it is evident that additional reasons are needed to explain why resources do not convert into higher fertility in industrialised populations.

Second, changing pay-offs to embodied capital investments in low-mortality industrial contexts are argued to generate a more extreme quantity-quality trade-off. That is, parents prefer a few highly educated, skilled offspring rather than a larger number of poorly educated, less skilled offspring. This trade-off is well established empirically in contemporary populations (see [35] for review and [38] in the current issue), and strongly aligns with Becker's economic theories. Such trade-offs are offered as an explanation for why an increase in resources has only very limited (and sometimes negative) effects on fertility in industrial societies: high-quality children offer greater returns on investment for wealthier parents than for poor ones [30], hence wealthier parents should expend more resources per child. Thus, even though, in physiological terms, individuals have the capacity to produce large numbers of children, the high costs of providing them with the kinds of embodied capital needed to compete successfully, combined with the distorting effects of extra-somatic wealth on people's preferences, results in small family sizes [31,36] that fall below that required to maximise fitness [36] (note that more recent work by Kaplan (and colleagues) extend these ideas by integrating both ecological-economic and informational-cultural theories; e.g., [39]).

3. EMPIRICAL FINDINGS AND THE MANY MEANINGS OF WEALTH

There has also been a continued empirical effort to examine the relationship between wealth and fertility. These studies differentiate more clearly between the different components of embodied capital, e.g., education and income, and show that these have differential effects on fertility. This makes clear that, contra Vining and Pérusse, a single measure or an arbitrary composite of wealth and status can be misleading: it is important both to specify clearly what measures are being used, and better yet, to control for different aspects of wealth (see [40] for a similar plea). Recently, Borgerhoff-Mulder and colleagues [9,41] have suggested that wealth can be divided into three categories: material, relational, and embodied wealth. Material wealth corresponds to Kaplan's extra-somatic wealth, while relational wealth accrues from the nature of an individual's social ties. Embodied wealth "encompasses the stocks of health, skill and productive knowledge embodied in people" ([9]; p. 345) (i.e., it contains elements of Kaplan's "embodied capital" and conforms to Becker's "human capital").

Most studies on industrial populations in behavioural ecology focus either on material wealth (i.e., income) or embodied wealth in the form of education. The effects seen are remarkably consistent, both within and between the sexes. Income is consistently positively related to fertility in men, but not in women (e.g., [6,7,42–45]), and seems to be driven mainly by poor men having a lower probability of marriage and hence remaining childless (e.g., [7,42,43,46]). The strength of the association between income and fertility is somewhat attenuated compared to pre-industrial populations, although its magnitude is higher than the selection gradients typically observed in animal studies (for any trait) [7]. Education in men is typically negatively related to fertility (e.g., [6,7,42,43]), but results vary [44,45]. In contrast, higher levels of income and education among women are associated negatively with fertility (e.g., [6,7,42–44]), although some studies mention a positive effect of income among highly educated women [27,42]. Overall, there is no clear indication of a "universal" negative association between wealth and fertility. There is, however, one factor common to all these studies that makes it inherently difficult to refute Vining's conclusions: all are based on cross-sectional data (something that, of course, also holds true for the studies of Vining and Pérusse).

3.1. Issues with cross-sectional samples

Cross-sectional samples, while highly informative, preclude any kind of causal interpretation regarding the relationship between fertility and wealth. Most importantly, one cannot exclude the possibility of reverse causality: income in later life may reflect the influence of parenthood, rather than vice versa. Indeed, empirical evidence suggests that women suffer a significant loss of earnings after the birth of a child (e.g., [47]; an "opportunity cost" that features heavily in Becker's US-based economic theory of fertility). Some of these effects probably reflect the fact that many societies conform to a "male breadwinner" model, where female income makes only a small contribution to household income (something exacerbated by early twentieth century employment policies; in the Netherlands and the UK civil service, for example, women were required to resign from their jobs when they married). Additionally, women who intend to have (many) children, or those that have recently entered motherhood, may choose less-

demanding, lower paying jobs [48]. Such effects make it difficult to use income measured at a single point (usually at the end of the reproductive life-span) to causally predict the number of children born. Cross-sectional relationships between female income and completed fertility may also reflect the way that labour markets discriminate against working mothers, rather than indexing an absence of resources being diverted into offspring. In contrast, a positive cross-sectional relationship in men could potentially reflect an increase in income following the birth of a child (e.g., [49]), which in turn could relate to positive discrimination toward fathers, or an increase in work hours to offset an increased need for resources.

Given these concerns, longitudinal data with repeated measures of both wealth and fertility outcomes can provide more convincing tests of the wealth-fertility link (see [50] for a similar point with respect to education). Such data can also provide greater insight into reproductive decision-making because they reflect the serial nature of fertility decisions [51,52], and because wealth may have differential effects at different parities (e.g., becoming a parent, having a third child)[11,53]; factors that are ignored when examining completed family size and wealth in later life.

4. A REVIEW OF LONGITUDINAL STUDIES

To begin tackling this issue, we conducted a review of the literature on material wealth and fertility. We focused on material wealth for two reasons. First, it is unclear exactly what association we should expect between relational or embodied wealth and subsequent fertility. Although lacking such forms of wealth is likely to be detrimental, it is unclear whether high levels of embodied and relational wealth should be associated with high fertility. For instance, how exactly should the prestige or status associated with being a doctor, net of her resources, predict fertility? In contrast, predictions are much more straightforward for material wealth: all else being equal, more resources should lead to higher fertility. Second, the evolutionary anomaly pointed out by Vining and others is that "superior resources" are associated with lower fertility, hence material wealth is the focus of most criticisms of an evolutionary approach.

This decision means that we do not consider education in any detail, despite the fact that, typically, it is negatively associated with fertility ([54]; see also above). Although education is often considered a wealth-seeking strategy, it is clear that education cannot be reduced to this alone: education brings many other individual advantages, including better health, more autonomy, and a broader perspective on life goals and opportunities. It is also clear that there is no simple substitution of education for fertility because societal structures mean that educational norms and opportunities overlap with (women's) most fertile years [50]. People who choose education may well intend to have a family (and even a large family; [55]), but fail to realise their intentions because of these institutional constraints. Furthermore, there may be differences across educational strata in reproductive strategies: there is evidence to suggest that highly educated mothers may possess a particularly intensive mothering strategy [56], whereas women with less education find more meaning in being a mother [57]. Safe to say, then, that decisions about education represent a combination of socioeconomic factors and ideas about the value of education that cannot be reduced to wealth alone or allow

education to be considered as a straightforward wealth-generating strategy. We do acknowledge, however, that, high investment in education, and the effect of education on an individual's behaviour, may sometimes be maladaptive.

In industrialised populations, material wealth can be accumulated through labour market income, intergenerational transfers, and government transfers [58]. For most, labour market income forms the major determinant of wealth (after consumption expenditures are covered). Although income is typically used to measures resources (mostly for reasons of convenience), this need not be an accurate proxy for accumulated wealth [40], and so we do not assume that high income also signals high levels of assets. Furthermore, we have shown recently that assets and income may have a differential effect on the probability of having a first, second child, or third child (and differently so across ethnicities and sexes; [11]).

We conducted searches using Web of Science to identify articles examining the relationship between wealth and fertility. We searched for the terms wealth/income/wage/social status/assets AND reproductive success/number of children/fertility AND longitudinal (15 searches in total). This did not constitute an exhaustive search because other search engines could also have been used, and no attempt was made to follow up on references included in the articles identified in each search. Our choice of search engine was, however, an ideal way to identify studies that were likely to compare closely to those of evolutionary scientists, and with which they might be familiar. Our review should therefor be seen as exploratory, presenting an illustrative snapshot of existing longitudinal data on the association between wealth and fertility. We generated 242 different articles without overlap. We were as inclusive as possible in our selection process: the only stringently applied criterion was that the study should contain a longitudinal analysis that dealt with the effect of wealth on subsequent (proxies of) fertility. Even so, this produced a sample of only 13 (5%) articles with the relevant longitudinal measures ([59–71]; see the supplementary materials for a description of these 13 studies and further description of the methods used).

There was some variation in outcome measures across the 13 articles we reviewed in detail, ranging from the probability of parenthood, second and third births, all births, and child mortality (which we included because reduced mortality might be a mechanism through which wealth can be associated with a higher number of children). It is important to mention that the sampling design of some studies potentially led to substantial problems of self-selection [72] (e.g., only sampling individuals who already had children), which serves to reduce confidence in the results (for further discussion, see [11,73]). In all cases, the measure of wealth reported was income (whether of respondents, spouses, or households). Only rarely was information provided on household assets. The studies covered four Western European countries (Finland, Sweden, Italy, UK), Russia, Australia and the US. All studies were focused on the second half of the 20th century, and in most cases, the study period also included the new millennium. Observed effect sizes tended to be rather small in magnitude (variation in outcomes, methodologies, and selection of subsamples prevent a straightforward aggregate effect size).

4.1. Wealth and fertility are likely to be positively related

We found that the relationship between wealth and fertility was much more likely to be positive than negative: there were 8 positive, 1 negative and 3 null findings (with the null or negative results often based on smaller samples, and less sophisticated methods; see supplementary material). One study showed that income positively predicted the second birth, but negatively predicted the third and fourth birth ([66]; see [11] for a similar example). Overall, it seems that economic factors are salient and influence people's fertility decisions in line with simple evolutionary predictions regarding the allocation of resources to reproduction. Despite continued debate surrounding the association between wealth and fertility, this finding is not particularly earth-shattering: it is no surprise that people assess their material wealth as part of their decision to have (more) children. For instance, recent research shows that around 50% of Italian couples report that they do not wish to have another child because of inadequate income [48]. This parallels closely the results of an earlier US study, which showed that 55% of the sample reported they would want more children if money was not a constraint [59](and this was particularly true for those with lower incomes).

The more interesting aspect of our review was the way it revealed that: i) a fuller appreciation of institutional structures is required to understand how and why the relation between fertility and wealth differs across nations requires [48,61–64,67,69], and ii) how uncertainty and economic (in)security rather than wealth per se are crucial to reproductive decision-making [48,62,63,67].

CONTEXT, HISTORY, AND CONTINGENCY: IMPLICATIONS FOR ECONOMIC EVOLUTIONARY THEORISING

Many studies from our literature review noted that institutional structures led to deviations from the common predictions of Becker's economic model of fertility [48,61–64,67,69]. In particular, there was a lack of support for the prediction that increased female labour force participation should decrease fertility because the opportunity costs associated with high wages should lead women to forego parenthood (or at least devalue it relative to income). When both female labour market participation and childrearing are facilitated through societal and institutional factors, parenthood is chosen more frequently (see also [10,74–77]).

The Swedish studies [61,66,69,71], for example, emphasise how governmental policies work to increase the compatibility of childrearing and paid labour for women. Beginning in the early 90s, generous parental leave was introduced, with benefits based on previous earnings. This can explain why income has a positive effect on fertility for Swedish women in particular: far from being a hindrance to childrearing, a certain basic level of income is seen as a prerequisite for beginning a family. At a population level at least, it is also interesting to note that, despite universal female labour force participation, Soviet-era Russia was also able to sustain fertility rates comparable to those of Western Europe. This was argued to be due to the provision of universal health care, day care and education [62].

In contrast to the Swedish case, Australia displays high levels of "institutional incoherence", where government policies promote gender equality and opportunity in the work place, but highly gendered expectations continue to exist in the domestic sphere (i.e., women are expected to do more domestic labour). This makes it almost impossible for women to combine work and family life [64], and a negative association between female earnings would not be surprising. Countries in which there is more equal division of both market and domestic labour have also seen an upswing in fertility [10,77], highlighting the importance of domestic labour in reproductive decision-making. Moreover, a recent study shows that in a period of increasing gender equality, the association between both male and female earnings and the transition to parenthood have increased in Denmark [74].

Thus, understanding the association between material wealth (or at least, income) and fertility in industrial settings requires a broader understanding of how domestic labour, and not just market labour, is allocated. More specifically, the institutional incoherence apparent in many countries means we should not be surprised to find a negative effect of female labour market income on fertility. When the demands of domestic labour fall mostly on women, time constraints alone may force women to choose between domestic versus market labour [78,79].

The inability of Becker's economic model to fully capture relevant aspects of reproductive decision-making across different cultures most likely reflects the fact that the model is itself highly "culture-bound" and limited to a specific time and place, namely, early post-war America. Indeed, Becker's model builds in at its source many of the features of the classic nuclear post-war American family, including its particular division of labour (where men are assumed to possess a relative advantage in the labour market) and stable long-term unions; clearly these features are not universal. If we relax these assumptions, we can potentially account for at least some of the cross-cultural variability we see. Yet, even in the US, Becker's model doesn't always hold up. For example, Musick et al [63] found that, contra Becker's model, female wages were not negatively but moderately positively related to fertility. Education was strongly negatively related to fertility, as predicted, but clearly this relationship could not be explained by its influence on wages, *sensu* Becker, given the positive effect of income on reproductive outcomes. In addition, the educational gradient was almost fully explained by *un*intended births and there was no major difference in the fertility desires of highly educated women compared to their less educated counterparts ([63]; see also [55,80]), although the former do tend to experience a larger gap between intended and realized births [80]. Thus, the fact that some aspects of Becker's theory no longer provide a good fit to behaviour within the US and beyond, suggest that incorporating its assumptions and predictions into a general evolutionary framework should be treated with a certain degree of caution.

5.2 Cultural history and contingent decision-making

Occasionally, historical data are also at odds with economic models of fertility, including embodied capital theory. During the British industrial revolution, for example, the introduction of new technologies did not increase the demand for skilled labour (at least

initially), and work in the labour market was often substituted for education [81]. The ability of children to engage in paid labour meant they continued to remain productive, even within the context of increasing industrialisation, rather than becoming the kind of "consumption goods", assumed by embodied capital theory. Indeed, Humphries [81] suggests that, in large part, child labour fuelled the engine of industrialisation in Britain, allowing for a much faster pace of economic growth than would have otherwise been possible. Most tellingly, her analysis suggests that it was institutional factors, such as educational reform and child labour laws (many of which were prompted and promoted by former child labourers), that changed employment dynamics, and led to children becoming less productive. At least in the British case, then, complex social and cultural changes play a crucial role in explaining how and why people made the shift from large to small families, and this cannot be explained by economic decision-making at the individual level alone. This suggests that we cannot ignore the contingent facts of history when attempting to develop models of fertility decline, although this historical component is not incorporated into current economic and behavioural ecological models. That is, institutional factors and historical processes are often taken as given by such models (perhaps envisioned as constraints; see also [51]), allowing individual reproductive decision-making to be predicted within a specific context. As institutional context represents a parameter of these models, it cannot, by definition, be used to predict the emergence of the institutions themselves (such as child labour laws, ideas of contraceptive use). As these institutional factors are clearly important for understanding patterns of fertility decline at the population level, it suggests that gene-culture co-evolutionary modelling is also needed to fully understand how and why fertility patterns shift downwards over time (see also [82] in this issue).

Finally, there are other features of child-rearing in contemporary industrial societies that suggest children are not simply "consumption goods" (see also [83,84]), and that economic considerations alone cannot account for why people do or don't opt for parenthood. For example, given the phenomenally high costs and few economic rewards of parenthood in societies like Italy, the issue at stake is why anyone would bother to have children at all, rather than why they have so few [85]. Becker's suggestion that children provide a form of "psychic utility" provides a superficial answer, but cannot account for why such utility exists in the first place. It is also apparent that, while fertility can be analysed as an economic decision, people's desire to have children is not wholly explained by these kinds of proximate cost-benefit analyses, instead parents wish to *produce* happy and fulfilled children (not simply 'consume' them, like other goods), and this task gives meaning to life in ways that do not map neatly onto notions of human and embodied capital [83]; people can also find meaning in their lives without children or wealth, and often actively forego both of these; people sometimes discover that raising a child is not as fun or fulfilling as they imagined, and this stops them from having more [86]; there is also strong two-child norm in some societies [87,88] which is argued to reflect a desire to avoid producing an only child—people who deviate from the norm by producing more than two children are often those who have two children of the same sex [88,89], and so wish to "balance" their families in some way (see [11] for further discussion). We realize that such cases are idiosyncratic, but they do illustrate that a narrow economic approach cannot adequately account for some of the variation that

exists. These factors further suggest that we may need to rethink the idea that small family sizes can be explained, at least partly, by a wealth-seeking/wealth-maximising psychological mechanism gone astray: it is apparent that people do possess a desire for children, and that, at least today, our psychology is not attuned solely to the accumulation of wealth and a desire to maximise resources (as all academics should be well aware of). More generally, such idiosyncratic behaviours are unlikely to be fitness-enhancing, and their existence therefore requires (evolutionary) explanation. Such cases are perhaps more easily explained by the diffusion of novel ideas, social learning mechanisms, and processes of cultural evolution [22,82] than by economic "rational actor" models of fertility (e g., the 'invention' and spread of the idea that having a child-free life is meaningful and fun, is made possible by, among other things, the development of fully reliable contraception, which itself entails a process of cultural evolution).

5.2. Uncertainty and fertility: what is wealth for?

Contrary to the implicit suggestions of Vining and Pérusse that resources do not constrain reproduction in modern society, it is clear that people do face economic constraints when it comes to child rearing, and that simplistic claims against evolutionary approaches are unfounded. It is equally obvious, however, that the effects of wealth are modest, and that both the mean and variance in the low-fertility high-income populations covered by our literature review are very low (see supplementary material; also [11,90,91]). This low variation is suggestive of a two-child norm [88,92], something that is well established in studies of people's preferences [87]. Thus, although resource availability continues to predict fertility levels, it is equally true that the very low fertility observed is unlikely to be adaptive, and indeed limiting fertility does not seem to increase fitness in later generations [30]. The super-wealthy are a case in point. Although the millionaires and billionaires of the Forbes 400 display some reproductive advantages [2,93], such as higher child survival [93], younger spouses (particularly when remarrying; [94]), and approximately 20-40% more children than the population average (i.e., about half a child more), the difference in their wealth is staggering, lying somewhere in the region of 5000% higher than average [95]. There are, then, literally hundreds of millions dollars that are not converted into offspring. This throws into sharp relief the slight reproductive advantage such extraordinarily wealthy individuals enjoy ([95]; a point also made by Vining [96] in a more recent paper). This being so, it is worth exploring in a little more detail how the wealthy view their resources, and how this influences fertility decisions, as a way to gain further insight into why fertility levels might no longer be fitness-enhancing.

For example, an ethnographic study by Cooper [97] conducted on 50 families living in Silicon Valley, California, documents a striking tendency for exceedingly wealthy families to continue accumulating wealth far beyond their immediate needs. In addition to using this wealth to furnish a high-consumption lifestyle, it is also revealed to be a strategy for ensuring an extreme degree of independence from the vagaries of life in modern US society. One respondent stated he would feel secure—but not rich—only once he had acquired 10 million dollars worth of investments: this would provide for both his children's and his own future regardless of market conditions, changes in health status and other

"security risks" ([97], p. 118). Cooper [97] suggests this is a rational response to living in a country where risk-minimisation is now seen as an individual, rather than a societal, responsibility, and where there is a perceived threat of globalisation to their offspring's chances of economic success. One could also interpret such findings in terms of a drive for relative status within a given reference group (i.e., being a millionaire only makes you feel 'poor' if your neighbours are billionaires), hence their decisions reflect runaway investments in wealth and child quality (that is, 10 million dollars is not actually needed to minimize risk). This interpretation is slightly complicated, however, by the fact that Cooper's respondents frame their reasoning in terms of the absolute cost of the resources needed to minimize risk for their entire family across the lifespan. That is, while the amounts are specific to a particular lifestyle, these appear to be realistic assessments of the cost of, for example, US health-care, and not some runaway process of keeping up with the Joneses.

At the other end of the US socioeconomic scale, those lacking material resources put their faith in family relationships as a source of security (in line with theories proposed by Draper [15] and Turke [16] that relational wealth may be key), "downscaling" what they consider as essential to their current and future wellbeing, given that the accumulation of material wealth and financial independence simply is not an option. At both the upper and lower ends of the economic scale, then, it appears that that risk-minimisation is crucial to understanding why people might limit their fertility: while the very poor attempt to manage risk in relation to exogenous economic shocks that constrain reproduction, the very wealthy attempt to eliminate risk altogether, which entails the generation of endogenous economic constraints on childbearing by assuming responsibility for all their offspring's financial risk across a large portion of the life span.

Many of the studies of our literature review highlighted the importance of economic (in)security in reproductive decision-making in a similar way [48,62,63,67]. In Italy, for example, religious influences and a traditional emphasis on family suggest that fertility should remain relatively high. Instead, Italy has one of the lowest fertility levels in the whole of Europe. Here, economic policies act against household and family formation, particularly for women [67]. The job market is characterized by long-term unemployment, low rates of social mobility and high insecurity, while heavily regulated maternity leave means that women are more costly to employ than men, which reduces incentives for employers to take on women [67]. As most Italians aim for a secure economic position before embarking on long-term choices relating to parenthood, the extended delay between finishing education (which itself has become greatly prolonged, as in other Western countries) and finding stable work means fertility is very likely to be postponed (or even foregone altogether)[48]. The emphasis on accumulating wealth in order to achieve greater stability and financial security in such populations therefore comes at cost to fertility—a deep irony in cases where economic stability is sought precisely because of a desire to produce and provide for a family.

Musick et al. [63] similarly suggest that the educational gradient in fertility in the US can be explained in large part by relational instability and economic insecurity. Specifically, conditions of economic uncertainty lead to a strategy of prolonged postponement of

childbearing among more wealthy and highly educated women, who perceive a certain level of income security is necessary before beginning to build their families. In contrast, women of lower socioeconomic position adopt a strategy of "judicious opportunism" [98], whereby they do not explicitly plan for children nor control their fertility, but capitalize on opportunities to build families whenever these arise. As a result, lower-educated and poorer women tend to experience more unintended pregnancies, and produce larger families, whereas highly educated women are more likely to produce smaller families than anticipated, or even experience unwanted childlessness (due to problems with conceiving at older ages). As with Cooper's [97] analysis, American women's decisions seem more responsive to economic security than to income per se, with higher education leading to a highly risk-averse reproductive strategy, and low education to a more flexible strategy. Thus, even within a population, it is clear that different strata employ different reproductive strategies, making it difficult to assess trade-offs accurately. Such variability also reiterates the importance of considering behavioural strategies within, rather than across, reference groups (something argued cogently by Mace [27,99] in an explicitly evolutionary context; this is also why using aggregate level data or failing to take account of socioeconomic strata may lead to false conclusions; [52,100]). Such findings also highlight the difficulty of equating education to wealth or at least access to resources.

6. THE COMPLEXITY OF (POTENTIALLY) MALADAPTIVE BEHAVIOUR

The (mostly) positive association between wealth and fertility in our literature review demonstrates that resources continue to constrain fertility decisions in industrial societies. We hasten to add, however, that the observed positive association does not lead us to conclude that contemporary fertility behaviour is therefore adaptive (i.e., fitness-enhancing). Rather, our message is that understanding the interplay between wealth and fertility among industrial societies is a complex business, and there is a need for a more detailed investigation of these relationships. The studies we have covered show, for example, that the neglect of domestic labour in economic models may help explain some of the observed patterns, as well as revealing that people may seek wealth not for its own sake, with the "unconscious" or "inadvertent" translation of wealth into fertility in hunter-gatherer life-ways (and a failure to do so in modern societies), but to ensure the security of their families in the face of ecological uncertainty [101]. In some cases, this may amount to the same thing, as the accumulation of wealth obviously ameliorates risk and uncertain outcomes. Indeed, some economists have even given definitions of wealth as a "variable that encompasses anything that may help an individual in coping with adverse occurrences", highlighting exactly this overlap [48].

Examinations of wealth and fertility in industrial settings might therefore benefit from drawing on those models that deal more specifically with risk and uncertainty (within both human behavioural ecology [101–103] and the social sciences [104,105]). The idea that people work toward ensuring their security also grants them greater agency than an 'unconsidered' or unconscious desire for material wealth, particularly in traditional societies where the idea of fertility as largely under physiological control seems to deny any capacity for foresight or planning (which would be at odds with human activity in other domains; see also [106]). One could argue that attempting to increase security in a

world of unpredictable human-manufactured risk could form part of a viable adaptive strategy but, if so, it would be one that is attuned precisely to the nature of risk in modern industrial society, and not simply the (slightly misplaced) application of an ancestral strategy to a new set of conditions. It is also possible, of course, that some evolved predisposition leads us astray, and that people over-estimate both the level of risk to which they're exposed under modern conditions, or the amount of wealth that is needed to prevent risk, both of which may serve to reduce fertility below the level needed to maximise fitness. This is, however, an open empirical issue.

It should be apparent that we are not suggesting the wholesale replacement of a wealth-maximising mechanism for a risk-minimising mechanism. On the contrary, our aim is not to advocate one way or the other, but to highlight the possibilities to explore wealth and fertility from a broader range of perspectives. Indeed, we consider it inherently unlikely that there will be a simple unitary explanation for why people fail to maximise fitness in industrialised populations, particularly because such populations can be so strikingly different from each other. We further believe that such mechanisms need not represent evolved psychological adaptations, but can also reflect the attunement of domain-general learning mechanisms to a given set of circumstances (e.g., [107]; mechanisms that are of course themselves evolved). Our argument is simply that the inclusion of risk minimisation as a human motivation, and the desire to attain some control over circumstances, adds an extra dimension to human decision-making that, currently, is not fully captured by theories that deal with wealth-maximization and status-striving alone.

Another important point is that the nature of the relationship between wealth and fertility does not, in and of itself, tell us very much about the nature of evolutionary processes and their applicability to modern society. The issue is more complicated than that, and we need to do much more to understand modern reproductive behaviour. As Symons noted, in his approving commentary on Vining's original paper: "People in the modern world fail to maximize fitness in innumerable ways, and there are innumerable differences between modern and natural environments" ([2]; p. 208). From this, he drew the conclusion that measuring fitness in modern industrial society, and testing hypotheses of current adaptiveness, serves very little purpose, arguing instead for a retreat to our ancestral past and the identification of the evolved psychological mechanisms that underpin modern behaviour (a view that is broadly held within evolutionary psychology). Whether such differences are truly "innumerable" is, of course, an open question, and it may very well be that many evolutionary relevant aspects of human behaviour have remained fairly constant (e.g., gathering sufficient resources, finding a suitable partner, raising a child to become competitive in the mating market; see also [19,108]). Moreover, although it is certainly plausible to suggest that we possess evolved psychological mechanisms that are not well equipped to cope with industrial environments, theories highlighting the drastically changed modern environment without specifying precisely what has changed and why, are of little explanatory value (a point also made by both Vining [2] and Pérusse [3]; see also [14]).

Although we acknowledge that modern populations differ from those in our evolutionary history (both recent and more distant), we draw the opposite conclusion to Symon's: measuring the components of fitness and studying modern-day behaviour are essential for determining whether or not these "innumerable differences" really do prevent us from behaving adaptively—after all, if fertility is never assessed, on what basis is the conclusion of maladaptive behaviour warranted? In the process of measuring fertility-decisions in a wide range of industrial (and pre-industrial) populations, we undoubtedly learn much about human decision-making processes (see also [11,19,73]), as well as potentially being able to identify putative evolved psychological predispositions; we believe such an approach is preferable to speculative hypotheses about our ancestral past and the a priori assumption of an evolutionary mismatch.

The changes seen in contemporary society should furthermore not be viewed as hindrances to an evolutionary analyses, but as essential components of the human adaptation that make us unique in the animal kingdom [109]. Burnside et al. [110], for example, in their analyses of the relation between energy use (indexed by body size), birth rates and fertility across species and across human populations, were careful to factor in the amount of extra-somatic energy used by human populations (i.e., the use of fossil fuels, and the infrastructure required to support these). Their analyses revealed that the energy use of a woman in the US today was equivalent to the metabolic rate of a hypothetical 30,000 kg primate, with a fertility rate similar to what one would expect for a primate of this size [110,111]. In other words, the low fertility observed in industrial populations is perfectly in line with that predicted on the basis of macro-ecological patterns of energy use, suggesting that we should perhaps be a bit more cautious in taking low fertility in industrial ecologies to represent a fundamental evolutionary anomaly.

CONCLUSION

Our review illustrates the need for evolutionary analyses to attend more closely to broader structural aspects that vary across industrial societies in both time and space: industrial society is not a monolith, and fertility decisions are biosocial phenomena that cannot be understood on the basis of ahistorical economic optimality models alone. While we have been critical of Vining's earlier conclusions, we are more sympathetic toward his recent argument [96] that human behavioural ecology currently does not provide any account for why the structure of the labour, or levels of social and gender inequality, should vary across industrial societies. Instead, certain aspects of modern society—like low levels of mortality and the high costs of raising children—are simply taken as given, and analyses then proceed by determining the nature of the trade-offs made under such circumstances. This is obviously interesting and entirely valid, but it cannot explain the process by which low levels of mortality and high childrearing costs arise in the first place. The focus on individual strategies as the unit of interest means we often fail to appreciate the influence of levels above the individual, and their impact on behaviour (but see [112,113]).

The real evolutionary puzzle that remains is why levels of fertility in industrial society are so low, despite a generally positive influence of resources on fertility decisions. Our study

cannot answer this question, but it does suggest that a greater focus on gene-culture co-evolutionary and niche construction models may pay dividends, as the existence of small family size norms, and preferences to forego reproduction altogether, are not predicted by standard evolutionary theory. The sociological literature may similarly be of aid: there is a rich and extensive body of sociological work that aims to uncover the ways in which economic uncertainty and gender inequality, along with the impact of globalisation, influence the human life-course (e.g., [105]) There is also an equally rich literature on economic history, documenting how and why modern-day economies take the form they do. Greater attention to the broader social sciences may help further our understanding of why low fertility norms emerge and persist, and the various routes by which similar outcomes are achieved. As the editors of this special issue suggest, an evolutionary perspective is essential for a complete understanding of human fertility behaviour. We agree, and would simply add that attention to historical processes and variability in industrial populations can contribute to such a perspective.

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