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Evolution and Human Behaviour: Helping to Make Sense of Modern Life

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Biological or genetic explanations of human behaviour tend to make people nervous, and not without reason. The promotion of eugenics and racist science by leading biologists and anthropologists of the nineteenth and early twentieth century produced some deeply shameful outcomes, culminating in the Nazis' appropriation of eugenic ideals to justify the Holocaust (Beckwith 1993; Marks 2017). Following World War II, UNESCO issued a statement disavowing the idea of biological/genetic differences in behaviour across different racial groups, emphasizing instead that all variation was environmental in origin (UNESCO 1952); we are all nurture, with no apparent nature. While understandable and, in some ways, laudable, such statements cannot erase the fact that we are biological organisms – for what else could we be? Like all other life forms, we are evolved creatures, the product of both genes and our environments (see Chapter 1). If you doubt this, try building an organism of any kind without using DNA. Clearly, then, the objections raised cannot be about biology or genetics *per se* – even the most dedicated environmentalist accepts that they will die without oxygen, and that babies are not delivered by the stork. Instead, resistance lies in the way that genetic and biological processes are theorized, studied and interpreted in the human context.

Similar objections are made to the application of evolutionary theory to modern humans (although there is no apparent problem applying it to the extinct versions of our genus). Again, there is a general acceptance that humans are evolved creatures while, at the same time, there is entrenched resistance to the idea that evolutionary processes influence contemporary human behaviour. At least some of this resistance reflects the way that evolutionary thinking has been applied to humans, rather than resistance to evolutionary thinking itself. In both cases, there remains a worry that labelling a trait or behaviour as genetic/biological or evolved is to suggest that it is immutable and predetermined. There is also the tendency for lay people to equate the words 'genetic' and 'biological' with the word 'natural', which can, and often does, lead to the conflation of what just happens to be the case with normative claims of what should be the case, otherwise known as the naturalistic fallacy (also see Chapter 1).

Evolutionary biology and genetics are, of course, inextricably linked – one of the most prominent definitions of evolution is that of changes in allele frequencies over

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time – hence concerns about genetic and evolutionary explanations go hand in hand. There is a distinction to be made between the two, however: talk of a genetic influence on behaviour does not, in itself, imply any kind of adaptive evolutionary explanation (or indeed any evolutionary explanation at all). Discussions of the value of evolutionary thinking as applied to humans thus address a different set of issues to those concerning the value of genetic studies of humans, including behavioural genetics. That is, although there is often the assumption that the heritable traits under study have been 'bred into' people, behavioural geneticists typically do not engage with the question of whether the traits are or were evolutionarily adaptive. Instead, behavioural genetics is concerned with the extent to which variance in a trait across people can be attributed to genetic versus environmental differences, and what such differences might mean.

In our view, the persistence of the nature-nurture debate into the twenty-first century often has more to do with a misunderstanding of the aims of behavioural genetic studies than with the application of evolutionary theory to humans in a broader sense. Consequently, in what follows, we first discuss briefly why studies in behavioural genetics seem to fuel the nature-nurture debate. We then go on to consider how evolutionary thinking can help improve our understanding of human behaviour, as well as showing why non-evolutionary thinking can sometimes go awry. Note that we make no attempt to be comprehensive in our assessment, rather we use a few key examples to illustrate the value of evolutionary thinking to real-world issues.

10.1 Understanding Interaction

One reason why nature and nurture just won't go away is because behavioural genetics seemingly promotes such a distinction (Tabery 2014; Fox Keller 2010). The reasons for this can be found in its origins in animal breeding and crop domestication. Artificial selection requires an accurate assessment of the likely response to controlled breeding; if most of the differences between individuals reflect variation in the environmental conditions encountered during growth and development, then artificial selection may prove ineffectual at producing a (suite of) desired trait(s). Hence, experimental and analytical techniques were developed that could partition the variance across individuals into its genetic and environmental components, enabling an assessment of the likely response to selection.

Of course, the analytical partitioning of variance in this way (explained more in Chapter 1) tells us nothing about the actual developmental process – the specific interactions of genes and environment – that give rise to a particular trait. Indeed, when used analytically, the notion of an 'interaction' is a purely statistical construct that complicates the interpretation of main effects (i.e. an interaction is a non-linear effect interfering with the attempt to cleanly partition the variance) and, as R.A. Fisher himself made clear, an inconvenience that can either be ignored (if the effect is very small) or else transformed to meet linear expectations (Fisher and Mackenzie 1923). This stands in contrast to the views of evolutionary developmentalists and geneticists, who are interested in the causal mechanisms that produce traits, and thus consider interactions between genes, gene products, the cellular environment and the broader ecological (and, in the case of humans, socio-economic) environment as both fundamental and central to any understanding of how a given gene might exert its effects (Tabery 2014).

This difference in how the term *interaction* is understood and used in behavioural genetics has helped generate the impression that the discipline is concerned entirely with separating nature from nurture, despite the fact that behavioural geneticists, just like developmentalists, recognize that traits are produced in the individual by complex interactions that make it impossible to cleanly assign the outcome to genes or environment.

As Tabery (2014) suggests, one way to reconcile these two views is to understand that what gets identified in population-based behavioural genetic studies are ‘actual difference makers’. That is, we can view all genes as potential difference makers, but only some will make an actual difference to the actual differences seen across individuals. Partitioning the variance then gives us some idea of whether *the* difference maker has been identified, whether we have identified *a* difference among *many* difference makers, or whether the difference made depends on environmental context (i.e. whether there is a gene-by-environment interaction). Once identified, actual difference makers can be studied by evolutionary developmentalists who seek to understand the causal mechanisms by which differences across individuals are produced. In other words, the two approaches can and do dovetail neatly. An emphasis on genes as ‘difference makers’, rather than ‘genes for’ particular traits, also lessens the temptation to see genes as somehow opposed to environmental influences, rather than operating in concert with them (Tabery 2014).

10.2 Understanding the Scope and Limits of an Evolutionary Approach

Evolutionary thinking applied to human behaviour is sometimes seen as addressing similar issues to those of behavioural genetics; that is,the extent to which a behaviour is influenced by our genes as opposed to our environment, combined with a more explicit assumption that those genes persist in the population because they enhance (or once enhanced) the fitness of their bearers. This represents a misunderstanding, if not an outright distortion, of an evolutionary approach, not least because the interactive process of development requires that organisms inherit certain stable features of their environment in addition to genes.

Given this, it makes no sense to insist that behaviour can be driven by genes alone, particularly not in large multicellular animals like ourselves. Rather, our nature is nurtured by our developmental environments. It is also important to note that demonstrating that a current behaviour is fitness enhancing (i.e. increases survival and lifetime reproductive success) does not entail that the behaviour also increased fitness in the past, nor does the failure to identify fitness-enhancing behaviour in contemporary environments mean that a trait does not have an evolved component. It is also the case that, even if one can demonstrate natural selection phenotypically (i.e. that individuals engaging in certain behaviours or possessed of certain traits experience higher survival and reproductive success relative to those without the trait or behaviour), it does not necessarily mean that adaptive evolution has or will occur; to do so, it is necessary to demonstrate a genetic response to such selection (i.e. one must demonstrate that the trait is inherited by offspring and increases in frequency in the population).

Stulp et al. (2015), for example, were able to show that height is currently under phenotypic selection in The Netherlands, with tall males and average height women experiencing higher levels of reproductive success (i.e. greater numbers of surviving offspring). The size of the effect was, however, very small, making it highly unlikely that natural selection alone explains much of the startling 20 cm increase in height shown by the Dutch over the past century (Stulp et al. 2015; Tarka et al. 2015). In addition, there was no evidence presented to support a genetic response to selection. What was apparent, however, was that the small effect of natural selection is acting in concert with the environmental conditions that promote increased height (e.g. widespread access to health services, low levels of social inequality, and a diet high in dairy products). This stands in contrast to the USA, where natural selection is acting to reduce height (Stulp et al. 2012; Byars et al. 2010), possibly mediated via a relationship between height and age at marriage and first birth (Stulp and Barrett 2016). In the US, natural selection therefore operates in opposition to environmental influences. Thus, even when effects are small, it is possible that they can help explain differences in trait values across different populations (Stulp and Barrett 2016).

Finally, the fact that social and cultural practices are themselves inherited and undergo transformation (see Chapter 3), and interact with genetic evolution, can make human evolutionary processes subject to more complex evolutionary dynamics (Richerson and Boyd 2005; Henrich and McElreath 2003). Evolutionary analyses must therefore be conducted with care, and interpreted cautiously, especially as ethical concerns mean that confirmatory experiments cannot be conducted.

10.3 Evolutionary Thinking as Puzzle Solving

So, how does evolutionary thinking help sharpen our understanding of human behaviour? One way is that it can help make sense of findings that would otherwise seem counterintuitive or puzzling. For example, a long-standing puzzle concerns the ‘Neolithic transition’ – the shift to agriculture from a hunting and gathering lifestyle. Agricultural lifestyles are associated with sedenterization, food storage, wealth accumulation and increased population growth (Piperno and Pearsall 1998; Price and Gebauer 1995). At the same time, the shift from hunting and gathering to sedenterization and cultivation demonstrably resulted in poorer health and increased mortality, as revealed by reductions in stature, poorer oral health, and evidence of diseases, such as tuberculosis, plague and syphilis (Cohen and Crane-Kramer 2007). Why then did agriculture succeed in replacing hunting and gathering lifestyles given that it poses a much greater threat to survival? The short, and flippant, answer is that natural selection does not care about health, only fitness. Of course, natural selection doesn’t care about anything at all, it is simply the outcome of a process of differential survival and reproduction. This, however, is the key point.

As Page et al. (2016) demonstrated, in a study of Agta people of the Philippines, a shift from hunting and gathering to settled agriculture is indeed associated with increased morbidity and mortality, including higher rates of child mortality. This is offset, however, by an increased reproductive rate, due to the energy savings that result from a more settled lifestyle. This results in a larger number of surviving offspring for settled compared to hunting and gathering Agta. Settled Agta thus display a shift in life history strategy, from producing a small number of high-quality offspring to producing a larger number of poorer quality offspring (Stearns 1992). This quantity–quality trade-off is precisely in line with life history theory, where an increase in child mortality (and hence a reduced chance of surviving to reproductive age) selects for an increased rate of reproduction, as this increases the probability that at least some offspring will survive and ultimately reproduce. Based on their findings, Page et al. (2016) therefore suggest that an analogous situation may have characterized the Neolithic transition: the cultural innovation of agriculture proved to be fitness enhancing and hence biologically adaptive, despite its costs in terms of human health. Thus, the invention and adoption of agriculture, as a cultural trait, is argued to have selected for a faster life history strategy, resulting in agriculturalists outcompeting hunter-gatherers, which in turn helped increase the spread of agriculture via a process of intertwined cultural and biological evolution. Applying an explicitly evolutionary perspective can thus help explain the otherwise counterintuitive spread of a behaviour that actively reduced the health and well-being of those who practised it.

Another example of this phenomenon is provided by Howard and Gibson's (2017) recent analysis of female genital mutilation or cutting (FGC) (defined by the WHO as the partial or total removal of the external genitalia or other injury to the female genital organs for non-medical reasons). FGC has clear and obvious health costs, both physically and psychologically (Iavazzo et al. 2013). It is equally obvious that it has negative consequences for women's reproductive success, due to the obstetric problems it creates (Banks et al. 2006; Adam et al. 2010; Berg and Underland 2013). Despite this, the practice remains widespread in many areas of Africa and the Middle East (where its prevalence ranges from 1% to 99%), and continues in the face of concerted and long-standing political efforts to eradicate it (Howard and Gibson 2017). One suggestion why eradication is so difficult is that cultural evolutionary processes take precedence here, promoting a behaviour that would otherwise fail to persist given its apparent negative biological fitness consequences for individuals. Specifically, the idea is that FGC persists either due to a conformity bias (i.e. where people copy the majority without regard to outcome) (Hayford 2005) or because it represents a co-ordination problem (i.e. men and women believe that FGC is necessary for marriage because the other sex demands it, and hence they reinforce the behaviour, despite the fact that both parties would be better off without it) (Mackie 1996). This has led to the suggestion that it should be possible, via a co-ordinated effort to change behaviour, to move a given population to a 'tipping point' whereby everyone switches rapidly from a cutting to a non-cutting norm. Howard and Gibson (2017) proposed that, in addition to considering these purely cultural evolutionary explanations, it was worth considering whether FGC confers fitness benefits on those adopting the practice, rather than simply assuming that FGC jeopardizes fitness; if so, FGC might prove to be adaptive within specific local ecologies and hence persist, despite its heavy costs in terms of female health and psychological well-being.

Using data from the demographic and health surveys (DHSs) of five West African countries, Howard and Gibson (2017) found that FGC did accrue fitness benefits to women, but in a highly frequency-dependent fashion. In areas with high FGC, cut women produced a larger number of surviving offspring at age 40 than women who had not undergone FGC. Conversely, in areas where the prevalence of FGC was low, women who had not been cut had a reproductive advantage over those who had been. Put into absolute terms, in areas with 0% FGC prevalence, cut women were predicted to have 0.34 fewer surviving offspring, whereas in areas with 100% FGC prevalence, cut women were predicted to have 0.44 more surviving offspring.

The persistence of FGC thus requires a more nuanced understanding of how cultural and biological evolutionary processes intersect. It is not simply the case that a strange and harmful idea has somehow become entrenched, persisting despite its fitness costs. Instead, performing FGC in an FGC-prevalent environment seems to promote the production and survival of offspring. As importantly, rejecting the practice under conditions of high FGC prevalence doesn't automatically lead to a boost in women's reproductive success (although, of course, they will be more healthy in other ways). Howard and Gibson (2017) argue that copying the majority in a given FGC environment might enhance a woman's 'mate value' in the marriage market, which may then translate into higher fertility and/or better child survival by ensuring better access to resources. FGC status relative to the majority may also be associated with entry into social networks that can provide enhanced access to resources and support, which could similarly be reflected in higher fertility and child survivorship.

These fitness-related differences are thus relevant to policy makers. Howard and Gibson (2017) suggest that the pattern shown in FGC prevalence across DHS countries is indicative of a move towards either 0% or 100% prevalence for a given group, that is, the tendency to copy the most frequent behaviour eventually leads one or other to dominate. If eradication policies were thus able to drive FGC below 50%, then a tendency to copy the most frequent behaviour, combined with the relative fitness-related benefits of doing so, should mean that FGC will gradually decrease over time. In other words, the notion of a sudden 'tipping point' that shifts the entire system rapidly is not the only mechanism by which FGC can be pushed into decline.

One final point to note here is that this study generated some negative responses on social media when published, as people interpreted the notion of fitness benefits to somehow suggest a tacit approval of FGC as a practice, or at least an attempt to deny its negative effects. What should be apparent is that Howard and Gibson's (2017) analysis of fitness-related benefits was aimed at providing an explanation of why eradication proves so difficult, and potentially identifying alternative means by which to drive the practice into decline.

10.4 Recognizing the Consequences of Our Actions

Another way in which evolutionary thinking can help sharpen our understanding of human behaviour is by predicting and explaining the consequences of certain courses of action that non-evolutionary approaches would not anticipate. Gibson and Mace (2006) provide one such example, with respect to the provision of labour-saving wells. Drawing on evolutionary life history theory, Gibson and Mace (2006) predicted that labour-saving initiatives designed to improve maternal and child health would also have the inevitable, but unintended, effect of increasing women's fertility, raising questions of whether such interventions represent an unalloyed good. Much like the Agta example described above, reduced workloads would automatically translate into more energy available for reproduction and, in the absence of reliable contraception, larger families.

Their study focused on a rural agro-pastoralist community in Arsi, southern Ethiopia, which suffered from both regular water shortages and food insecurity. Between 1996 and 2000, tap-stands were introduced into a number of villages as part of a water development scheme. During the driest months of the year, this reduced the amount of time women spent carrying water from just over three hours to only 15 minutes per day. The water development scheme thus represented a natural experiment into how shifts in women's workloads and energy budgets influenced fertility. As predicted, women with access to taps were three times more likely to give birth in any given month relative to women without access, and water access was also associated with a 50% lower risk of children dying. However, there was no evidence to suggest that the intervention improved maternal and child nutritional status and health outcomes – the ostensible aim of the initiative. In fact, children in villages with access to water were significantly more likely to be malnourished, and access to water taps was unrelated to women's body fat levels. Although the intervention was successful at reducing child mortality, it came at the cost of increasing childhood malnutrition. Gibson and Mace (2006) suggest this latter effect could be due to increased sibling competition for limited resources (as seen in other studies, such as Lawson and Mace 2009) or, perhaps more likely, as a consequence of reduced mortality among low-birthweight babies (which, potentially, could represent a relaxation of selection on low birthweight, if such a trait were heritable). The effects of malnutrition were seen only in the children born following tap installation, rather than across all age groups, suggesting that improved water access increased the likelihood of low-birthweight babies coming to full term and surviving critical early periods of childhood.

Another example of a potentially misapplied intervention is the fortification with iron of infant milk formula. Infant iron stores are largely accumulated over the course of gestation, and decline in the first few months post partum in breast-fed infants, as human milk is low in iron ($0.2–0.5\,\mathrm{mg\,l^{-1}}$). This decline generally has been viewed as pathological, thus resulting in a debate over the appropriate amount of iron fortification in infant formula: this can range from 4 to $12\,\mathrm{mg\,l^{-1}}$, so even the lowest levels are an order of magnitude higher than those found in breast milk. Quinn (2014) has suggested that we have things the wrong way around, and high levels of fortification may, in fact, be pathological. Her hypothesis is that iron depletion over the course of early life is an adaptive response to the onset of weaning and the introduction of non-milk foods. Many bacteria require iron for growth and replication, so low iron levels may limit the duration and severity of any infection to which an infant is exposed during the introduction of solid foods. Selection may thus have favoured mothers who produced low-iron milk, along with offspring with decreased iron stores at weaning, as this would increase the chance of surviving the weaning period. Although we currently lack the data needed to fully test this hypothesis, Quinn (2014) cites data from a number of studies demonstrating that low levels of iron intake during infancy were not associated with higher levels of anaemia and, in one study, low levels of iron were associated with both lower rates of infection and greater head growth. In this same study, iron supplementation did nothing to further reduce the risk of anaemia, but was associated with higher rates of gastrointestinal disease and reduced growth (Domellöf et al. 2001). Contemporary fortification practices may therefore undermine these adaptive mechanisms, and increase the chances of children falling ill, rather than providing them with a health-giving boost.

The application of an evolutionary perspective thus helps makes sense of why technological developments aimed at improving maternal and infant quality of life can backfire potentially. These examples also have policy implications. For example, introducing technological advances that fail to consider impacts on women's fertility may exacerbate problems of population growth, so development initiatives need to include provisions for family planning and access to effective contraception. Similarly, if low iron levels are adaptive in early infancy, this has implications for government and WHO guidelines concerning the nutritional content of infant formula.

10.5 Thinking Differently about Fertility Control

Contraceptive uptake itself is also something that has been studied via an evolutionary perspective. This often strikes people as rather odd, given that the availability of reliable contraception has been given as a reason why people no longer maximize their fitness in modern, industrial societies. For example, Lutz et al. (2006, p. 172) state that 'through the introduction of modern contraception, the evolutionary link between sex drive and procreation has been broken and now reproduction is merely a function of individual preferences and culturally determined norms' (see also Vining 1986; Pérusse 1993). Indeed, in our experience, people often assume that the term 'natural fertility population' refers to those in which contraceptive uptake is low or absent, when it simply refers to a lack of parity-specific control of fertility (crudely speaking, there is no target family size or 'stopping rule'). Natural fertility populations can and do practise fertility control (but often with less reliable methods than the contraceptive pill) and there is widespread evidence for the use of contraception and abortifacients reaching all the way back to antiquity (Colleran and Mace 2015; McLaren 1990; Riddle 1994).

Attempting to control fertility should not, therefore, automatically be seen as a break between sex and procreation, rendering evolutionary explanations irrelevant. The existence of fundamental trade-offs between investment in continued reproduction and investment in other domains, such as growth, bodily maintenance and care of existing offspring, prevents any organism from producing the maximum number of offspring of which they are physiologically capable. Accordingly, attempts to control certain aspects of these trade-offs, namely the number and timing of offspring, should be seen as integral to human life history and parental investment strategies, regardless of whether these are achieved by physiological or technological means. Indeed, in some cases, a life history perspective provides a more satisfactory explanation than one that assumes that contraceptive uptake reflects only the transmission and adoption of new arbitrary cultural norms.

For example, Alvergne et al. (2011) found no evidence that membership of social or spatial networks influenced the initial uptake of contraception by Ethiopian women during the early stages of a demographic transition. Rather, the initial adoption of contraceptives was a means by which women could regulate their fertility and increase parental investment per child (Alvergne et al. 2013). Indeed, 96% of the women adopting contraceptives for the first time had already reproduced: women had nearly four children on average at the point of contraceptive uptake (Alvergne et al. 2011). Moreover, those children born before their mothers adopted contraception were less likely to die before the age of five than the children of non-contracepting mothers. It is therefore plausible to argue that the use of contraception can have fitness-enhancing effects, via increased investment in offspring and increased survivorship. Looking at patterns within women, before and after they adopted contraception, it was found that mothers were less likely to reproduce after short interbirth intervals once they had adopted contraception, but this had no subsequent effect on their children's mortality risk. This latter result possibly reflects the fact that increases in contraceptive uptake among women also coincided with other developmental initiatives in the region that served to reduce child mortality.

Overall, then, women in this sample apparently began using contraception to lengthen the spacing between births, enabling them to invest more in their current children. Moreover, this was a product of individual behavioural innovation by women, rather than by social diffusion of new (arbitrary) cultural norms (ultimately, this must, of course, be the case, given that new norms require a source from which they can diffuse). Alvergne et al.'s (2013) results thus speak to theories concerning fertility decline more generally. While shifts in cultural norms of desired family size undoubtedly contribute to fertility decline, it is also possible that, as Alvergne et al. (2013) point out, when mortality declines before fertility, and family size increases more rapidly than expected, the use of contraceptives may, in fact, represent adherence to a stable, locally adaptive cultural norm for intermediate family sizes, albeit via novel, technological means (see also Winterhalder and Leslie 2002; Carey and Lopreato 1995).

Of course, there are certain situations in which the tight control of fertility clearly does not serve to maximize fitness: voluntarily choosing to remain childless and investing resources in luxury holidays or other consumer goods is one such example (but it is also important to remember that individuals of all species fail to maximize their fitness at times; such variability is, after all, the engine of natural selection). Equally, the demographic transitions that have taken place over the course of the nineteenth and twentieth centuries in Europe and North America, where populations have shifted from high-fertility/high-mortality regimes to low-fertility/low-mortality regimes suggest that people no longer maximize fitness in the industrialized west (Sear et al. 2016). These shifts in behaviour have been argued to reflect the adoption of cultural norms, and/or evolved psychological mechanisms aimed at optimizing parental investment in children, which lead to extreme quantity-quality trade-offs in modern industrial settings, neither of which serves to enhance fitness (see the papers in Lawson et al. 2016 for a thorough exploration of these issues).

Even in such apparently clear-cut cases of maladaptive behaviour, some caution is warranted, however. Burnside et al. (2012), for example, argue that the dramatic increases in non-metabolic energy use of the last 10 000 years, which made possible the agricultural, industrial and technological revolutions, can and should be factored into assessments of human life history as well. This is because the fecundity and reproductive rates of human females are not constrained by their metabolism as in other mammals, but instead vary with total energy use (Moses and Brown 2003). Burnside et al. (2012) thus demonstrated that if our 'extrasomatic energy' in the form of fossil fuel consumption were to be considered as a contribution to human metabolism, then the total energy use of a modern-day American woman would be equivalent to that predicted for a hypothetical 30 000 kg primate. Seen in this context, the lifetime reproductive output of modern industrial humans is precisely that predicted by life history theory for an animal of such vast size, thereby complicating the notion that modern industrial humans are capable of rearing many more children than they actually produce (and according to DeLong et al. (2010) such considerations also mean it is unlikely that the rest of the planet will undergo a demographic transition in just the same way: the energy cost of doing so far exceeds the fossil fuel energy that will be available, and consequently cannot slow population growth).

The relationship between energy use and fertility is not only apparent when cross-species comparisons are made, but also across cultures and across time within human cultures. Indeed, the amount of extrasomatic energy used by a population is a good predictor of fitness components like fertility, child mortality and age at first reproduction (Burger et al. 2011). That is, these traits seem to be highly plastic, and respond readily to increases in extrasomatic energy. As Burger et al. (2011) also show, however, the same is not true of lifespan and age at menopause; these are only weakly related to energy use, and appear to be more constrained physiologically. What this means is that some industrial humans have a much shorter reproductive lifespan than predicted for an ape of our (King Kong) size. That is, the increase in age at first reproduction (which follows from an increase in extrasomatic energy, and hence an effective increase in body size) is not compensated for by a longer period of productivity, as life history theory would predict. This may be a reason why industrial humans' fertility falls to below-replacement levels (i.e. fewer than two children per woman) in some instances.[1] Having said this, the greater plasticity of age at first birth and fertility, both of which show moderate heritability, suggests selection could continue to act – by favouring lower age at first birth, for example – and fertility levels could increase in the future.

There is no reason, then, to believe that current 'lowest low' levels of below-replacement fertility are irreversible. Indeed, as Burger and DeLong (2016) point out, there is no genuine theoretically grounded demographic principle for accepting this to be the case; it merely follows from the assumption that sustained economic growth will continue, and returns to human capital will remain high. The application of evolutionary theory to demographic issues provides one very powerful means to understand contemporary shifts in fertility behaviour, and hence to generate more accurate population forecasts.

10.6 Modern Contraception and Mate Choice

Contraceptive use has also been studied in the context of mate preferences and mate choice, and the work we discuss below also helps reinforce our point concerning the need for a careful and cautious interpretation of particular findings. In this case, evolutionary thinking was used to provide a new perspective regarding the unforeseen side effects of oral contraceptives (OCs) on women's sexual functioning.

Ever since the introduction of the oral contraceptive pill, concerns have been raised about its negative effects on women's libido. It has proved difficult, however, to identify the mechanism responsible for such effects, and it is equally difficult to predict which women will suffer from them (Burrows et al. 2012; Sanders et al. 2001). One possible evolutionary explanation, known as the 'congruency hypothesis', is that OC use influences aspects of the mate choice process, with the result that a woman's attraction to her partner may change over time if she either discontinues or begins taking the pill, because her

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[1] Some caution is needed here, however, as the life history predictions are made at the individual level, whereas the relationship between energy use and fertility occurs at the population level. We thus need to be aware of the ecological fallacy: relationships at the aggregate level do not necessarily translate to the same relationship at the individual level (see Pollet et al. (2014, 2015) for more details).

current contraceptive status no longer matches her status during partnership formation (Roberts et al. 2012, 2013, 2014; Alvergne and Lummaa 2010). There is evidence to suggest, for example, that the major histocompatibility complex (MHC) exerts an influence on mate preferences (specifically those related to odour), with preferences shown for MHC-dissimilar partners (Wedekind et al. 1995; Havlicek and Roberts 2009). The use of OCs has been shown to shift preferences towards MHC similarity, however (Roberts et al. 2008). Thus, couples that form when a woman is taking OCs should be more likely to show MHC similarity. If the woman then stops taking OCs as the relationship develops, this may lead to a shift in women's preferences for MHC dissimilarity, a reduction in attraction to her partner, and a loss of libido, one that is mediated by her use of OCs but is not directly caused by the pill in and of itself (Roberts et al. 2012).

In support of this, Roberts et al. (2012) found that women who were using OCs during partnership formation, and then went on to have their first child with this same partner, scored lower on a number of measures of sexual satisfaction with their partners compared to non-users, and they also rated their partner's body as less attractive. In a second study, Roberts et al. (2014) presented a more powerful test of the congruency hypothesis, and more convincing evidence of its effects. Here, they asked both members of a couple to assess their relationship satisfaction, and obtained detailed information on women's current and previous OC use. In this way, they could obtain a measure of congruency between a woman's OC use during partner choice and her current OC use, and test whether this better predicted her relationship satisfaction than either OC use during partner formation or current OC alone. This design also allowed Roberts et al. (2014) to explore different routes to congruency in OC use (i.e. users who remained users versus non-users who remained non-users). Finally, asking male partners for their views enabled Roberts et al. (2014) to investigate how congruency in OC use affected men's versus women's assessments of satisfaction.

In line with the congruency hypothesis, women's sexual satisfaction was predicted by congruent OC status, but congruency did not affect women's non-sexual satisfaction, nor did it predict men's satisfaction with their partners. The latter finding thus supports the idea that changes in women's OC status directly influences women's satisfaction, rather than being a consequence of changes in men's attraction to their partners due to a shift in her OC status. In addition, there was moderate evidence for an interaction between previous and current OC use, where non-congruency via either of the two possible routes was associated with lower satisfaction than women whose status remained congruent. Importantly, neither previous nor current OC status alone could explain any aspect of women's sexual satisfaction. These results were thus argued to explain why the negative effects of OCs on women's libido and behaviour often prove elusive; understanding the effects of hormonal contraceptives requires an assessment of how women's OC use changes in relation to partnership formation, and potential shifts in women's hormonally mediated partner-specific levels of attraction.

A recent replication of Roberts' 2014 study, however, failed to find any support for the congruency hypothesis (Jern et al. 2018). The study was conducted on a large sample of Finnish women (n = 948), which gave it sufficient statistical power to detect the effect sizes previously reported. The only effects found were differences in sexual satisfaction between women who consistently used OCs and those who did not, with consistent OC users showing higher sexual satisfaction scores than non-users (and no effect at all for relationship satisfaction scores). Jern et al. (2018) concluded that the congruency effects reported in Roberts' previous study most likely arose from the fact that there was an unequal distribution of current OC users among the congruent and incongruent user groups. That is, in the congruent user group, participants were equally distributed between current users and non-users, but in the incongruent user group, 115 of the participants were current non-users (i.e. had stopped taking OCs following partnership formation), and only 35 participants were current users (i.e. had begun taking OCs following partnership formation). As a result, the difference between the groups that was taken to be an effect of congruency in OC use may simply have reflected consistency in OC use: the congruent group had far more consistent users in it than the incongruent group.

As Jern et al. (2018) point out, studies of the congruency hypothesis received widespread attention in both the academic community and the mainstream media (including *Time*, *Women's Health* magazine and the *Guardian* newspaper). It is therefore possible that these studies may have influenced women's decisions regarding contraceptive use, or influenced their perceptions of their likely long-term relationship success. These new findings, which suggest that the congruency effect may not exist, illustrate both the vital importance of replication and the dangers of accepting effects as real in advance of replication taking place. At the same time, a single non-replication does not necessarily rule out the existence of the congruency effect (e.g. it is possible, if unlikely, that Finnish women alone are not susceptible to these effects). Further replications are needed before we can conclusively state that the congruency hypothesis fails to explain the pill's negative effects on libido, and we should consider the jury still out, rather than accept any firm conclusions one way or another.

10.7 Evolution and Assisted Reproductive Technologies

Humans have not only developed technologies for limiting or controlling fertility, but also for overcoming the problem of infertility in both men and women – something that is estimated to affect ~10% of couples in industrial nations (Gnoth et al. 2003), and ~80 million people world-wide (Vayena et al. 2002), with the highest prevalence in the so-called 'infertility belt' of central and southern Africa (Inhorn and van Balen 2002). The first 'test tube baby', Louise Brown, was conceived via *in vitro* fertilization (IVF) and born in 1978. Since then, over five million children have been born via assisted reproductive technologies (ARTs) (Inhorn and Birenbaum-Carmeli 2008), and in some countries, 4% of all newborns are conceived by IVF (Kupka et al. 2014). ARTs now include not just IVF for women with blocked fallopian tubes, but also intrauterine insemination (IUI), insemination by a donor (DI), and intracytoplasmic sperm injection (ICSI) to combat male infertility, the latter of which involves the injection of 'weak' sperm directly into oocytes. In addition, egg donation and gestational surrogacy are increasing in frequency.

As well as challenging traditional views of kinship (children can potentially have three parents), ARTs expand the option of parenthood to gay couples (via donor insemination or surrogacy), and shift what people consider to be the 'natural' response to infertility. In Europe and America, where adoption was once seen as the most acceptable, and natural, way for infertile individuals to become parents, there is an increasing desire for people to 'chase the blood tie' (Ragoné 1996), and use ARTs to conceive their own biological children. This is now regarded as the more 'natural' option, even though it requires a massively choreographed technological intervention by a wide variety of medical professionals (Thompson 1996, 2005). There are also increasing numbers of postmenopausal women over the age of 50 achieving IVF pregnancies using hormonal assistance and donor eggs (whether their own previously frozen eggs or those of a younger woman) – a technological, extrasomatic means to circumvent the fixed limit to the human reproductive lifespan identified above. Perhaps more than any other human invention, ARTs blur our long-standing notions of nature and nurture, biology and culture. In principle, embryos can be 'designed, stored, exchanged and implanted in any womb' (Hanevik et al. 2016) and reproduction is therefore likely to become increasingly independent of age, gender, and sexual orientation (for a comprehensive and fascinating review of how ARTs affect not only our understandings of kinship and parenthood, but also gender equity, social inequality and bioethics, see Inhorn and Birenbaum-Carmeli 2008).

Thus, although the link between sex and reproduction has been broken by ARTs, they nevertheless have the capacity potentially to influence evolutionary processes. IVF involves a number of artificial environments, procedures and selection criteria that are distinctively different from those that occur in the womb. Under natural conditions, large follicles with high sensitivity to both follicle-stimulating hormone (FSH) and luteinizing hormone (LH) are selected, and there is a single oocyte that undergoes ovulation. These pressures are relaxed under conditions of IVF, where all but the very smallest follicles are suctioned out, and a number of oocytes are subsequently selected for further manipulation. In turn, this manipulation exerts an array of new selection pressures, including the ability to withstand needle puncture and removal of cytoplasm in the case of ICSI (Hanevik et al. 2016).

The same is, of course, true for spermatozoa. In the absence of human intervention, successful spermatozoa are excellent long-distance swimmers, that can make their way through the vaginal mucus and locate the oocyte via chemotactic means, whereas the IVF selection processes favour sprinters, that can swim faster over shorter distances and rapidly penetrate the egg. In the case of ICSI, the normal selection pressures are almost entirely relaxed, as low-motility spermatozoa that clearly could not fertilize an egg under typical conditions are given the opportunity to do so, and do not even need to possess the capacity to penetrate the egg (Hanevik et al. 2016).

Conversely, IVF imposes new selection barriers on laboratory-created embryos. These bypass the barrier imposed by the fallopian tubes, but such embryos need to make it through the computerized process by which embryo morphology and development are visually analysed and assessed. As Hanevik et al. (2016) point out, this means that computer algorithms now comprise a selection barrier that has no analogue to the normal process of embryo transport to the womb. Similarly, oocytes and embryos are increasingly subject to freezing – another laboratory process that must be withstood if they are to be selected for future fertilization and implantation. The increased robustness required of IVF spermatozoa, oocytes, and embryos may come at the cost of other traits that we have yet to identify (Hanevik et al. 2016); this is not to say the outcome will be negative or detrimental, merely that we need to recognize that how these new selective regimes represent a particularly potent form of gene-culture coevolution; these new technological interventions occur at the point where natural selection has operated at its strongest.

Finally, Hanevik et al. (2016) point out that ARTs select for certain people to reproduce by these technological means. They give the example of Norway, where a woman with a BMI of 25 will qualify for state-funded IVF treatment, but one with a BMI of 45 will not. The high cost of IVF therefore represents another form of selection barrier to those who cannot access public funds, and selects against those with low income, both within economically developed countries, as well as setting up a differential between low- and high-income nations.

One possible – if extreme – outcome of ARTs, then, is that we will generate a distinct population of humans that is dependent entirely on IVF to reproduce, with certain traits linked to infertility no longer coming under selection, or experiencing a form of positive selection. Both endometriosis (which leads to blocked fallopian tubes) and polycystic ovary syndrome (which causes anovulation) are known to be heritable (Treloar et al. 1999; Vink et al. 2006), such that an increased prevalence of IVF may lead to an increased prevalence of these conditions in particular populations. Similarly, boys conceived by ICSI are more likely to show a malformation of the penis known as hypospadia (Ericson and Källén 2001) (in a neat historical twist of fate, the very first record of artificial insemination was performed to assist a man who suffered from this particular condition) (Home, 1799).

As Hanevik et al. (2016) point out, we are still very far from understanding the potential long-term evolutionary consequences of ARTs, given that the oldest IVF individual is still only in her early forties. ARTs do, however, force a recognition that humans are becoming biologically, as well as culturally, dependent on our own technology. Hanevik et al. (2016) suggest that, to date, an evolutionary perspective may have received limited attention because of the implications that ARTs allow ‘inferior’ individuals to reproduce, leading to odious eugenics-style arguments against it. Obviously, no such normative conclusions are warranted, not least because natural selection does not lead to the ‘best’ or ‘fittest’ solutions in the colloquial sense, but simply to those outcomes that are most successful in a given environment. The main message is that, as we mentioned at the start, an evolutionary approach requires an certain degree of caution, and an appropriate level of humility.

10.8 No Free Lunch

We can illustrate this latter point with a final cautionary tale concerning the treatment of stomach ulcers. We now know that *Helicobacter pylori* is the cause of stomach ulcers, thanks to the efforts of Barry Marshall and Robin Wallace, who won the Nobel Prize for Medicine in 2005 for this discovery. *H. pylori* is one of the most prominent gut bacteria we acquire during childhood and, among other things, is involved in the regulation of gastric hormones, affecting gastric pH (Blaser and Falkow 2009). Over 50% of all cells found in the gastrointestinal niche are *H. pylori* cells.

When Marshall and Wallace first suggested that the cause of stomach ulcers was bacterial, back in the early 1980s, the idea was met with scepticism: no one believed that any bacteria could survive the acidic environment of the stomach. When experiments that attempted to infect piglets with *H. pylori* failed, Barry Marshall, in a marvellous display of self-experimentation, (in)famously drank some cultured *H. pylori*, determined to prove that it was the cause of peptic ulcers (he expected this to occur years later).

Within a few days, he began to feel nauseated and about a week later developed major gastritis, and *H. pylori* was cultured from his stomach. After two weeks, he began taking antibiotics, the inflammation cleared up and he thus demonstrated that the gastritis was due to the bacterium (you can read the whole story in Barry Marshall's Nobel Prize speech) (Marshall and Warren 2005; Marshall and Adams 2008). Following this discovery, *H. pylori* has also been shown to substantially increase the risk of a particular kind of stomach cancer (Blaser et al. 1995; Helicobacter and Cancer Collaborative Group 2001).

Given its status as a human pathogen linked to devastating and fatal diseases, pharmaceutical companies have spent a lot of time and effort developing a means to eradicate *H. pylori* from the human gut. Why wouldn't we want to remove a potential source of mortality, particularly one as nasty as gastric cancer? As Blaser (2006) points out, however, the fact that all mammals have one or other kind of *Helicobacter* species residing in their guts, combined with our own long history of coevolution with *H. pylori*, should perhaps have given us pause. Genetic studies of *H. pylori* have shown that diversity among strains decreases with distance from East Africa, much like human genetic diversity does, suggesting that *H. pylori* has coevolved with humans over the last 60 000 years (at least) (Linz et al. 2007). *H. pylori* is thus found across all human populations, and (until recently) its prevalence was around 80%, but only a relatively small number of people suffered any ill effects due to pathogenic strains.

The potential consequences of ridding our microbiota of its most dominant player didn't feature in these efforts to 'cure' us of our *H. pylori* infections but, as Blaser (2010) notes, we are now receiving something of a wake-up call, as we begin to recognize some of the costs associated with our 'disappearing microbiota' (Blaser and Falkow 2009). For example, Sonnenberg et al. (2010), in a study of over 78 000 US patients, found that the absence of *H. pylori* was associated with the presence of a condition called Barrett's oesophagus, which involves abnormal changes in the cells of the lower oesophagus, a condition that can turn malignant and lead to oesophageal adenocarcinoma (EAC) (a particularly nasty form of throat cancer). Barrett's oesophagus, in the first instance, develops from a condition called gastro-oesophageal reflux disease (GERD), which also seems to be linked to the absence of *H. pylori*. As *H. pylori* is the most common microbe, it is also possible that it isn't the loss of *H. pylori* itself, but of another species that occurs at lower density, and so isn't picked up by such studies. *H. pylori* could therefore just be a marker for the loss of some other micro-organism.

Over the past century, then, the prevalence of *H. pylori* has been dropping steadily among economically developed countries to the extent that less than 6% of US children now carry it, and the incidence of both peptic ulcers and gastric cancer has dropped accordingly in the adult population (Blaser 2006). At the same time, GERD, Barrett's oesophagus and EAC have all increased. Essentially, we seem to have swapped one set of unpleasant, but curable, diseases for another set of equally nasty, but currently less curable, diseases, and generated a new selection pressure on humans.

10.9 Conclusion

The examples we have covered here illustrate that modern evolutionary explanations go well beyond the kinds of caricatured biological/genetic explanations that critics fear. Evolutionary theories enable us to test well-formulated hypotheses and offer convincing explanations for a variety of human traits and behaviours in contemporary populations, particularly those that seem counterintuitive. Most of our examples here have concerned fertility in one way or another, and this was no accident. Fertility lies at the core of evolutionary biology, and using an evolutionary lens offers an effective aid to understanding the reproductive strategies of contemporary humans, including how and why contraceptive uptake occurs, patterns of fertility decline through history and across the globe, as well as forcing the recognition that current levels of fertility need not persist indefinitely, and that technological interventions in the reproductive process are likely to have evolutionary consequences.

Moreover, we hope to have shown how human agency and conscious decision making do not, in fact, allow us to transcend our biology in the way we often imagine: active human decision making designed to improve health and increase well-being has itself generated a new set of biologically based health and population problems we now have to solve. An even broader lesson is that an evolutionary perspective on human behaviour, especially in contemporary populations, means more than just focusing on individual circumstances. We must also account for the cultural historical and sociological factors that influence how governments and industry act in the face of technological advances of various kinds.

The final take-home message, then, is that an evolutionary approach to human behaviour requires an understanding of the entanglements of nature and nurture, culture and biology, and has much to offer the study of societies that differ widely from those of ancestral populations. Via a variety of 'extrasomatic' capacities, including extensive social learning, our use of tools and technology, and the harnessing of fossil fuels and other forms of energy, we can and do adapt to the environments we create for ourselves much faster than is usually believed.

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