



# HUMAN EVOLUTIONARY DEMOGRAPHY

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# 3. A Biologist's Perspective on Human Evolutionary Demography

*Bobbi S. Low*

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Human evolutionary demography has produced striking advances by applying the lens of fitness maximization to demographic data. This approach has strong parallels and links to life history theory, which concerns life patterns (e.g. age at first reproduction, age-specific fertility and mortality) and behavioural ecology, which examines ecological and social influences on behavior. Both those fields focus primarily on non-human species. In addition to clarifying fitness thinking within demography, human evolutionary demography is helping those of us in related fields to deeper understanding of our own disciplines, partly because we know so much in detail about human lifetimes and their diversity. Evolutionary demographers often can bring multiple scales of analysis and multiple kinds of data to bear on research questions, enriching our broader understanding. In the past, those of us who studied non-humans have not typically been able to do this — but seeing the value of such work, in at least some cases, for some species, today we may be able to do better. Finally, there is some potential for this cross-disciplinary approach to have real, and real-world, value in terms of making sensible and realistic policy.

I am a biologist who stumbled into human evolutionary demography. When my son was two months old and I was a single mother, my field work was on digger wasps that hunt fast-flying robber flies. Schlepping my son, a portable crib and gear to the field site was awful (mostly my son screaming, reflecting how he hated this). I had an epiphany: I needed something to work on that I could do on the computer, after he was asleep. This led, in the 1970s, to my first work on humans. Then, six years later, at the birthday party of a colleague's nephew, the grandfather — an evolutionary scholar — said to me “with your interest in resources and reproductive success, you should meet another parent here who has worked with the Swedish Demographic Database.” This was invaluable advice: the Database, originally designed so that schoolchildren could trace their lineages, had never had someone bring a set of testable hypotheses to explore, and I found a gold mine! An analyst there, who became a good friend, was amazingly helpful in getting the files organized. I discovered something I had never suspected about data gathered without reference to one's hypotheses: they can't be biased by one's approach to questions — but they also sometimes fail to be useful for one's important questions.

That I should shift into demography is not as odd as it might seem, because my focus has long been on life history theory and behavioural ecology; evolutionary demography (with some language shifts) encompasses both. Life history focuses primarily on non-human lifetime patterns — demographics like age-specific fertility and mortality — which are shaped by the trade-offs all organisms face.

Behavioural ecology takes analysis to a finer level, focusing on how environmental conditions shape both demographics and behaviour. And *human* evolutionary demography tackles all of these concerns for the species about which we have, arguably, the best and most detailed data.

All three of these approaches examine the costs and benefits of different life history/demographic patterns under varied environmental constraints: age at first reproduction; trade-offs of current versus future reproduction; semelparity (one-time reproduction)/degree of iteroparity (how often reproduction is repeated); clutch or litter size; trade-offs in offspring size versus number; and more. The languages used differ across fields somewhat, as do the emphases, but cross-fertilization across perspectives has been fruitful — and I think has become even more useful today. I attempt nothing like a complete literature review; other chapters will do that admirably.

Here I hope to highlight facets of evolutionary demography that help those of us in related fields to deeper understanding of those fields: the importance of multiple scales of analysis, and of multiple kinds of data; the value of really deep knowledge in a particular species for enriching broader studies, and the value of evolutionary demographic analyses in the wider, applied policy world.

Organisms invest time and energy in growth, maintenance, finding mates, raising offspring. For many expenditures, what is spent on one endeavor cannot be spent on another: energy invested in an offspring, for example, cannot be used to improve one's own condition. Which expenditure is most effective at any moment depends in large part on environmental conditions (Stearns 1992; Roff 1992). It is worth noting that both Stearns and Roff included human data for comparisons when available.

The three approaches — life history theory, behavioural ecology, and evolutionary demography — are strikingly parallel; their evolutionary and ecological bases are deep and clear. As noted by Sear et al. (2016), all three seek *ultimate* explanations for the variation we see in life history variables. They contrast, in that life history comparisons tend to be broad in scope, comparing multiple species; behavioural ecology tends to focus on ecological influences on behaviour, often for one particular species. However, until recently (Borgerhoff Mulder 1991; Cronk 1991a), neither of these considered human patterns. Human evolutionary demography produces rich and detailed data on past and present populations within one species — humans. Evolutionary demography not only uses this perspective, but also commandeers the social science “bottom up” approach in examining variation — looking at proximate triggers or cues for behaviour. The combination is powerful.

Human life histories and demography may show more intraspecific variation than we (think we) see in other species. We have, for example, broad cross-cultural data for more than a thousand societies (many of which are traditional), and we have modern transnational data for about 175 nation states. This complexity and variation within a single species suggests, I think, that evolutionary demography can both enrich and refine life history theory and behavioural ecology.

Although scholars in the various fields were not well connected when pioneer evolutionary demographers began to apply the lens of fitness maximization to demographic issues, these pioneers converged on problems central to life history theory and behavioural ecology — which were then still developing as well. The work accumulated was revealing (see Sear et al. 2016 for an excellent review). Alice Clarke, then a doctoral student, and I were struck by the commonalities, leading us to write a review of papers testing evolutionary hypotheses with demographic data (Clarke and Low 2001). It was rewarding to find real progress.

Sometimes, in those early years, papers read like 'standard' demographic papers. The evolutionary and ecological hypotheses that drove the questions might be hidden — but they were there, and were important in beginning to infuse demography with evolutionary thinking. At the time, I was dubious, but I now think such 'stealthy' approaches were really helpful: do outstanding demography, link results to things evolutionary scholars think are important, but do not “lead with your chin” by aggressive labeling (further, I am hearing from colleagues today that stealth is still useful in getting published and in changing minds). I think the new lens helped shift the thinking of “classical” demographers. I remember showing a “box” in Daly and Wilson's (1983) *Sex, Evolution, and Behavior* to a demography colleague who was methodologically expert. The box took an evolutionary lens to an excellent paper by the colleague; the writing was aimed at people already using an evolutionary perspective. He became agitated, and forcefully shut the book. We said no more about the topic, but in a very few years, as evolutionary demography papers accumulated, he was moved to write about an evolutionary perspective arising from his own data (Knodel et al 1997).

The work Dr. Clarke and I found focused primarily on traditional and historical societies; it covered basic topics in life history, and included work on strategy-environment matching both in the past (historical forces) and in the present (current utility). The authors we reviewed were anthropologists, economists, demographers and biologists — all expanding horizons in demography by examining human demographics through an evolutionary lens — what today might be called part of behavioural ecology. I still have a preference for the term “ecological demography” (Low, Clarke, and Lockridge 1992, Low 1993) rather than “evolutionary demography” because almost all extant work is about how well particular strategies perform under specific ecological and social conditions — that is, behavioural ecology. We seldom have the relevant genetic information to infer evolutionary change over time. In biology, the term “evolution” often concerns changes in gene frequency over time — and even now, few studies on human adaptive responses can meet that criterion.

Many of the topics Dr. Clarke and I found in 2001 tended, unsurprisingly, to be rather straightforward parallels to the sorts of questions raised by life history theory and behavioural ecology papers on non-human species:

- age-specific fertility (Daly and Wilson 1997);
- relationships between resource control and/or status and reproductive success, especially for males (Chagnon 1979; Irons 1979; Hill and Hurtado 1996; Kaplan et al. 1995; Betzig 1986) and family lineages (Hughes 1986; Turke 1989);
- quantity-quality trade-offs in fertility (Becker and Lewis 1974; Mace 1998, 2000a);
- the rarity of twins (Lummaa et al. 1998; Haukioja, Lemmrtyninen, and Pikkola 1989; Gabler and Volland 1994);
- infanticide (Daly and Wilson 1984, Hrdy 1992, Hill and Hurtado 1996) and child abuse and neglect (Daly and Wilson 1984);
- infant and child survivorship as a function of parental socioeconomic status and a child's sex (Mace 1998, 2000a);
- optimal birth spacing (Blurton Jones 1986);
- sex-biased investment (Trivers 1972; Charnov 1982; Cronk 1991b);
- the impacts of migration on lineage success (Clarke and Low 1992).

In each case, the issue of optimization — finding the most reproductively effective strategy, given environmental constraints — was paramount, as it remains today. These papers, and more, represented new and fertile investigations in anthropology and demography. They connected previously separate fields, and had strong ties to work by biologists on other species. We found scattered, less concentrated work on additional topics: sex differences in remarriage; impacts of illegitimacy on survival and reproductive success; and alloparental care.

Another ubiquitous concern in these early papers was that of trade-offs, imposed not only by ecological conditions, but also cultural practices. Even that long ago (2000–2001) there was well-grounded work that, while focusing on important life history topics, integrated these with cultural practices (e.g. optimal fertility and inheritance (Mace 1998, 2000a) and the impacts of marriage system on child mortality (Strassmann 1997)) that can affect the relative advantage of alternate strategies. The issue of trade-offs is as old as Darwin. Like Lawson and Borgerhoff Mulder (2016) and others, I have argued that demographic transitions are really about how much investment in children matters in improving their competitiveness, and that increased per-child investment usually results in fewer children because of the trade-offs. This is simply a re-phrasing of the quantity-quality trade-off raised by Darwin (1871, I: 319):

The only check to a continued augmentation of fertility in each organism seems to be either the expenditure of more power and the greater risks run by the parents that produce more numerous progeny, or the contingency of very numerous eggs and young being produced of smaller size, or that are less vigorous, or subsequently not so well-nurtured.

Of course, evolutionary anthropologists and demographers (e.g. Borgerhoff Mulder 2000) and some economists (e.g. Becker and Lewis 1974; Becker and Tomes 1976) have recognized and highlighted this quantity-quality trade-off; though I have found no other reference as old as Darwin.

The costs and benefits of trade-offs may differ for different kinds of individuals. Suppose there is a trade-off between offspring size and number: a beetle female cannot make as many large eggs at a time as small eggs — but really large beetles can nonetheless make a lot of very large eggs (biologists call this the “phenotypic correlation”). That is, specific individuals with extraordinary resources may not be so constrained as others (e.g. Lessells 1991). Similarly, what you spend on your house, you cannot spend on a car (you have finite resources) — yet really wealthy individuals can afford both a fancy house and a fancy car. In modern societies with high inequality (in wealth, health access and more), this may mean, for example, that wealthy individuals can have many children *and* invest fully in all. There can be circumstances in which familial wealth (or other contributions) reduce the trade-offs (as above: when more resources mean more, still highly-invested, offspring). As Easterlin and colleagues (Easterlin 1978; Easterlin and Crimmins 1985) argued, we may be back to: “more resources leads to higher fertility.”

Further, it is clear that such cultural influences as religious and legal rules (pro- or anti-fertility) and individuals’ assessment of their status relative to their parents, their cohort and others in their current environment influence fertility decisions. Thus, we will continue to see great variation. The task now is to understand that variation (e.g. Macunovich 1998) — and here, I think evolutionary demographers lead the pack.

Though we attempted a thorough review, Dr. Clarke and I missed some important papers (e.g. Mace 2000b); we even missed analyses of clearly ecologically-driven issues like optimal foraging (e.g. Smith and Winterhalder 1992). We weren’t alone; unintentional biases in citations were common, often reflecting difficulties in covering literature, for example, from other countries, or different

communities of scholars (see Sandstrom 2001). This problem has been ameliorated over the years by services like Google Scholar, Academia.edu and Research Gate, so that today, thorough coverage of papers on a topic is easier to achieve, and failure to be complete is more easily discovered.

### What Is Exciting Today

Early work in evolutionary demography drew on principles from biological theory, particularly optimal foraging theory, life history theory and behavioural ecology; the concept of (biological) fitness maximization was then largely unknown in classical demography. As a result of the progress and explosive expansion over time of evolutionary-minded papers, we are at an exciting juncture today in many ways.

Human evolutionary demography is in a position to inform and deepen our understanding in several fields, from some presumably 'simple' and unquestioned principles in life history theory to fertility policy. Current evolutionary demography can draw on more kinds of data than earlier work. Often, it can provide analyses at several scales, from transnational analyses to analyses of individual patterns within a single population or sub-population. Models are more sophisticated today, and potentially more useful. It is not my intention to review modern advances: again, other chapters in this volume do that. But I will explain why these advances excite me.

### Finding the Right Scale of Analysis: It Depends on the Question

Because scholars are interested in human data for many reasons, and demography is a broad subject, papers' emphases can vary greatly. In non-evolutionary demography, both single-population and large-scale comparisons were common, but in some cases, we would say today that the match between scale of analysis and the questions asked could be improved. An example is work by Birdsall (1980; see also Birdsall and Griffin 1988); these papers were broad comparisons examining fertility across nations and completed fertility within nations by wealth category for four countries. Birdsall's analyses were important, in the service of understanding fertility and poverty in the developing world. Yet as a behavioral ecologist I was struck, and initially confused, by the emphasis on transnational comparisons. The transnational data looked (loosely) as though fertility was higher when resources were more limited — the opposite pattern from that found in other species, in traditional societies and in historical societies.

I eventually realized that (as you will find obvious) these were spurious patterns for the questions that interested me: the reproductive patterns of families in such strikingly different ecologies, as it were, were simply not comparable for evolutionary questions, though they clearly had policy relevance (Birdsall's focus). Similarly, Vining (1986) and Pérusse (1993), who took similar approaches, argued that cultural success and biological fitness were unrelated or negatively related. Stulp and Barrett (2016) have noted that such cross-sectional comparisons were inappropriate for analyzing wealth-fertility patterns.

Birdsall's within-country comparisons by wealth quintile showed patterns that by now will be familiar to many of us: in some nations, wealthier families had more children than less wealthy families, in others, mid-income families were larger. Today we recognize that there is no single pattern; results depend on conditions (more below). In Birdsall's work, there was no real conflict in the empirical data, but the conclusions drawn more or less ignore the within-population results — yet these are important for questions of interest to us.

It is important, then, to recognize that different scales of analysis are appropriate for different questions. How does one decide on the appropriate scale for a question? In comparative analyses from both non-human life history/behavioural ecology and human evolutionary demography, both large-scale and small-scale comparisons can be useful. Early on, there were occasional mismatches that confused at least some of us. As biologists sought to make large generalizations, they typically compared across species. Sometimes evolutionary demography papers do too, with important results (e.g. Galdikas and Wood 1990). Most comparisons of human populations today do a good job of matching scale to question.

Comparisons across human populations, or across individuals within a population, may highlight complexity that is masked by cross-species comparisons. These approaches offer rough parallels to general life history theory and behavioural ecology, which similarly look at variation among individuals that belong to a category within a population or across conspecific populations in different environments. I suggest below that the detailed understanding brought by more localized studies can usefully inform the broader arguments.

The lack of an evolutionary lens in non-evolutionary analyses of demographic transitions led, I think, to a relatively narrow focus. For example, the well-studied historical particulars of the Western European transition led non-evolutionary demographers at first to imagine that industrialization was *the* driving force in lowering fertility; this confusion of correlation with causation led to consternation when developing nations such as Thailand (e.g. Knodel, Havanon, and Sittitrai 1990; Knodel and Wongsith 1991) underwent rapid demographic transitions without industrialization. In Thailand, the important proximate factor turned out to be the benefits of secondary education (which was not free) in getting good stable jobs so one could marry and have children. Parents discussed how many children they could afford to put through secondary school, and fertility fell dramatically, from eight to ten children per couple to roughly two, in about ten years.

This importance of the reproductive utility of particular statuses or resources, and the requisite costs to acquire them, are widely recognized in evolutionary demography. Even early classic evolutionary anthropological or human behavioral ecological studies of traditional societies routinely found that even for ostensibly egalitarian groups lacking any formal currency, a man's skill (e.g. hunting among the Ache: Hill and Hurtado 1996), social/political status and power (e.g. among the Yanomamo: Chagnon 1979) mattered to reproductive success. When physical resources exist (e.g. cattle, sheep or goats among the Kipsigis: Borgerhoff Mulder 1988, 1990; or money from market transactions e.g. among the Turmen: Irons 1979) they are used.

The bottom line is simple: whatever resources, tangible or intangible, can improve reproductive success, they will be so employed. Because these societies (and most traditional societies) are polygynous, it is males who are mostly affected. Even apparent exceptions actually follow the rule. Among the Mukogodo, parents invest more in their daughters than their sons (e.g. in food distribution or trips to the clinic: Cronk 1991b) — is this an exception? No. In this case, the Mukogodo are the poorest and least powerful people in the region they inhabit. Mukogodo men are seen as undesirable by families from other groups in the region; plus, Mukogodo men can rarely manage the bride wealth demanded. But Mukogodo *daughters* can marry into families from higher-status groups, so it pays reproductively to invest more in daughters for Mukogodo families.

Certainly, in traditional societies for which we had data, increased resource control (and/or status) typically led to increased reproductive success, primarily for males (just as for other



species studied). Historical data reinforce this pattern, even in socially monogamous societies. Wrigley and Schofield's (1981) detailed non-evolutionary work found that marriage and birth rates in England historically fluctuated, tracking the economic environment. I similarly found in nineteenth-century Sweden that fertility and marriage rates fluctuated in response to the ecological pressures of shortage and abundance of resources — transitions were local and reversible; I could find no evidence of a monolithic, irreversible transition in Sweden (e.g. Low and Clarke 1983). Nonetheless, even though divorce was unknown, wealthier men had, through remarriage after a wife's death, higher lifetime fertility than poorer men (see summary in Low 2015). Voland (e.g. 1990) similarly found that wealth enhanced fertility for German men. The variation we observe actually clarifies the fact that fertility is, in fact, influenced by ecological factors.

Some of my biology colleagues may well recoil from placing humans in this “bin” with other species. We all agree that natural selection operates on humans as well as other animals, but for complex behaviors such as fertility timing, humans can be and are influenced by cultural factors (religion, cultural norms) and other group-level influences (e.g. policies at governmental levels, which shape individual costs and benefits). Surely this invalidates any comparison? I would argue that what we are asking is: are responses, however mediated, ecologically appropriate (e.g. does fertility fall when resources constrict)? The major difference between genetically-dictated responses and “cultural” (etc.) responses seems to be that responses arising from phenotypically plastic conditions (whether “if-then” genes or conscious, culturally-mediated decisions) is that phenotypically plastic responses can react quickly (e.g. Cavalli-Sforza and Feldman 1981). So whether we are asking about genetically or culturally mediated responses, the core question remains valid: do responses make ecological sense? There is one caveat, however: cultural responses that are ecologically inefficient can persist for some time in humans, because humans have such a long generation time. All we can really say is that cultural norms that are costly in terms of dramatically reducing reproductive success will never become and remain the most commonly-observed behaviours, and will tend to be replaced over time — e.g. the Shakers.

So far, what I know reinforces my understanding that, because the real question is about selective appropriateness, we are finding that resilient human responses are, indeed, typically selectively sensible norms. What a pleasure today to see how evolutionary demographers with broad and deep data on post-transition societies (e.g. Stulp and Barrett 2016; Stulp et al. 2016) tease apart the relationships between wealth and fertility (generally positive), finding that considerable variation makes ecological sense.

Again, the scale of focus must be appropriate for the questions asked, and evolutionary demographers are able to integrate data across multiple scales. They continue to demonstrate that work at multiple levels, with well-matched levels of analysis to questions, generates real understanding.

### Integrating Multiple Kinds of Data Brings New Insights

A particularly fine development has arisen today because evolutionary demographers are using multiple approaches that complement each other. Empirical field data (analyzed through an evolutionary lens), large secondary data sets and lab work each bring different dilemmas to a researcher, but, I think, each also offers unique insights. Together, they enrich our knowledge at multiple levels. Over the years, I have found that field work (I have worked on non-human species from kangaroos to digger wasps) leaves one at the mercy of field ecological conditions, but can

also lead to new insights simply because you are watching intensely, and ecological conditions can change. Lab work (e.g. calcium metabolism in a number of species) allows a more targeted analysis, from biochemical and physiological aspects to DNA analyses, but can sometimes be tedious, and (especially in shared labs) vulnerable to unforeseen contamination. And secondary analyses of existing large data sets, such as the nineteenth-century Swedish demographic data, can give us windows into worlds we otherwise could not approach. However, because the data were likely gathered for questions other than yours, they can be frustrating to work with.

## Evolutionary Demography Can Enrich Biology

I think the multi-faceted findings from evolutionary demography can inform and deepen biological analyses that exist at the broad, multi-species level of comparison. Here is an example. Biologists have understood for a considerable time that life expectancy at birth or hatching ( $e_0$ ) predicts much about reproduction, and that it is the impacts of *extrinsic* mortality (not especially related to individual behaviour) that matters. The shorter the life expectancy, the (relatively) earlier reproduction (AFB, age at first birth) will begin; this typically means that total fertility rate (TFR), and resulting age-specific fertility, will be higher for populations, or lineages, experiencing short life expectancy at birth.

The classic paper (Harvey and Zammuto 1985; see also Figure 5.10 in Stearns 1992) cleverly transformed data to compare life expectancy at birth and age at first birth for warthogs and rabbits, chipmunks and meadow voles and more; the results were striking. Of necessity, they used existing data, which were (and are) hard to come by. As a result, the comparisons made two crucial assumptions. Firstly, any population will adequately represent the species: a chipmunk is a chipmunk is a chipmunk. Secondly, relationships are at equilibrium and do not change rapidly. These are relatively common assumptions in ecology.

But are these assumptions accurate? I can hear evolutionary demographers chuckling already. The wealth of data on human populations can help to clarify the complexities sometimes overlooked in big generalizations. The basic relationship (above) holds for humans as well as other species: the lower the life expectancy at birth ( $e_0$ ), the earlier reproduction begins, and the higher fertility is likely to be throughout life (Low et al. 2008; Low et al. 2013; see also Daly and Wilson 1997). However, across human populations, the relationship is non-linear, and there is extraordinary variation. Further, it is clear that neither of the assumptions made by Harvey and Zammuto holds for humans (Low 2013, Figures 11.2 and 11.3).

Low et al. (2008, 2013) found that no single population would adequately represent the relationship between  $e_0$  and AFB for humans as a species. We could not capture all the variation, because the samples were national averages. Even so, the variation is dramatic: in a sample of 130 nations for which there were data for both  $e_0$  and AFB, AFB ranged from 18.2 to 29.6 years, and  $e_0$  ranged from 31.3 to 82.2 years.

The wealthiest, longest-lived populations fit the generalization well, and had we only examined them, we could have produced a graph much like that from Harvey and Zammuto. Life expectancy at birth was a good predictor of age at first birth (Low et al. 2008: when life expectancy was  $>60$  years: regression results were  $\beta=0.757$ ,  $R^2=0.58$ ,  $p<.0001$ ). In part, this reflects the strong influences of cultural norms (more below) on reproductive practices.

In contrast, the greatest variation in AFB was in the poorest countries (called by the United Nations Development Programme “Human Development Index 3”: “HDI-3” in the data used).

These societies approximate those termed the “Bottom Billion” by Collier (2007). In these countries, one would likely predict constraints to be greatest, just as appears to be true for other species: we expect life expectancy at birth to be short. Yet AFB could vary strikingly within a narrow range of  $e_0$ . Rwanda and Chad, for example, had almost identical life expectancy, but AFB was 18.2 in Chad (which was extremely poor and suffered drought), and 22 in Rwanda, which endured genocide and civil war so severe it may have led to state collapse (Low et al. 2013). Here, the sources of mortality are important: early childhood deaths as in Chad affect life expectancy differently from adult deaths (principally HIV as well as genocide in Rwanda: Low et al. 2013, especially Figure 3).

What about the second implicit assumption: that life expectancy is in equilibrium? If life expectancy is not stable over time, the relationship between  $e_0$  and AFB may also be in flux, and mismatched. We found (Low et al. 2013, Figures 1, 2) that, indeed, life expectancy varied dramatically from 1955 to 2000 in essentially all countries, though the particular patterns of changes fell into several different groups. There were nine strongly different patterns of changing life expectancies (2xBIC ranged from 22.1–313.4; when this measure is  $>10$ , differences are considered very strong, so these patterns are extremely strong: Jones, Nagin, and Roeder (2001)). Here is a clear example of the ability of evolutionary demography to refine older, broader generalizations. And note that this analysis still lumps non-comparable populations together, as if ‘nation’ represented one population. We still have a lot to learn.

The lesson for biologists here, I think, is that just as picking one population at one point in time is inappropriate to represent “human fertility”, it is almost certainly true that not all populations of chimpanzees or chipmunks are identical, although I recognize that the logistic difficulties can be extreme in studying multiple populations of non-human species. And, in fact, we do know about some inter-population variation in a few species, such as chimpanzees and orangutans (e.g. Whiten et al. 1999, Watts 2008, van Schaik et al. 2003). Such fleshing out of the selective inferences from specific inter-population variance can enrich our understanding. Here, evolutionary demographers have much to offer biologists.

### In the Wider World

Often the work of life history, evolutionary demography and behavioural ecology can seem remote and academic. I think the opposite is true: only by focusing on the ultimate pressure of fitness maximization — the driving force shaping behavior — as well as fleshing out the proximate details of just *how* environmental pressures shape behavior, is it possible to get beyond our past of simply seeking correlations, to uncover what actually influences behaviour.

Human fertility is related in complex ways to a considerable number of factors such as wealth, income, education, certain kinds of female labor force participation and more. These relationships differ in least-developed and more-developed countries: ‘development’ typically involves more female education and more paid female participation in the labour force.

Once constrained largely by ecological influences, fertility today may be most strongly influenced by cultural factors: norms and religious beliefs (as in fights over abortion rights), and human oddities that probably count as ‘ecological factors’ because they contribute to an environment in which arguments succeed or fail (like policies such as tax structures that affect the costs of children, and more). In nations around the world, policies are being made constantly that affect women’s lives, both directly (e.g. access to health care, or rules about fertility control) and indirectly (e.g. policies affecting the costs and benefits of women’s individual choices). But many, perhaps most,

such policies have unintended consequences, both in their direct and indirect effects. Who better to analyze proposed policy than scholars who not only measure and understand proximate drivers of behaviour (child-care availability, etc.) but who also understand evolved human biases — which can contribute to the failure of the best-intentioned proximate policies? I suggest that evolutionary demographers are ideally positioned to make a positive difference in this arena.

Historical events can leave their footprints, complicating matters. Once (e.g. in the 1960s and 1970s), fears of overpopulation (e.g. Ehrlich 1968) were intense. Governments at various levels, and individuals, responded in various ways, again with unintended consequences. South Korea, in response to concerns about population growth, established policies that today have resulted in arguably the world's lowest total fertility rate, and there is concern about ageing and loss of workers resulting from this policy overshoot.

Fertility rates and total fertility vary around the world today. The UNDP's Human Development Index rankings assess health (life expectancy at birth), education (years) and living standards (e.g. GDP per capita). As we would expect, fertility is strongly patterned with the HDI measures of development. The TFR for the most-developed nations averaged below replacement, but is well above replacement for the least-developed nations. Of course, this does not reflect within-nation variation; it does, however, suggest that governing bodies will have quite different interests in influencing fertility."

The most developed nations comprise much of the HDI rank 1 and they have below-replacement fertility, as well as delayed ages at first birth, and high levels of women's education: the correlates you would expect. The proximate causes of declines vary. In contrast to the Korean experience above, Japan's low fertility appears to have been driven first by individual choices rather than formal policy: after World War II, women appeared to shift to stop childbearing well before menopause (lowering TFR), and later to delaying both marriage and fertility. This resulted in a marked decline in fertility among women in their twenties, and a slight increase in fertility among women in their thirties (Tsuya 2015). Japan has, from the mid-1990s through the 2000s, implemented a number of policies aimed at helping parents of preschool children balance their domestic and work responsibilities, for example increasing child care opportunities and more. But the problems remain: despite pro-natalist policies, Japan's TFR remains below replacement.

Policy has typically addressed proximate influences: e.g. expanding educational and professional opportunities for women. But gendered divisions of labour, a major force in our evolutionary past, persist as an influence: in Japan, even though women are employed, they continue to do roughly five times as many hours of household work per week as do men (Tsuya 2015).

Many low-fertility countries hope to implement pro-natalist policies, but the complexities of fertility and its covariates suggest that more unintended consequences are likely to follow. Getting input from scholars who understand both proximate and ultimate influences on our behavior should help to reduce unintended negative consequences. Further, not only fertility rate, but other important demographics, such as sex ratio, can be affected. Well-meant Indian efforts to empower women, with the further goal of improving treatment of their daughters, backfired: the more educated and wealthy were the families or mothers, the more daughters suffered discrimination (Mahalingham 2007; Das Gupta and Visaria 1996).

Here is another difficulty in making policy: implementation of policies assumes agreement on policy goals — but from the level of individuals and communities to government institutions, agreement is often lacking. Perhaps the United States is an extreme in terms of polarization today, but consider the fights, at all these levels, about funding for Planned Parenthood, which

provides information, outreach and reproductive services for almost five million people a year (<https://www.plannedparenthood.org/>).

Information, we hope, can help alleviate disagreements in which the difficulty is that facts are lacking. Policies affecting fertility, if successful, will have downstream impacts that benefit different actors. Lee et al (2014) brought a demographic lens to the questions raised by low fertility: who benefits, and who does not? Because there are multiple economic interdependencies that link both public and private intergenerational transfers across age, the impacts of transfers, and the policies that affect them, can differ. Thus, low (and falling) fertility can drive rapid population aging. Lee et al noted that almost half (48%) of the world's population then lived in countries in which the total fertility rate (TFR) is below replacement.

In their analysis of forty countries, Lee et al. found that fertility well above replacement would benefit government budgets; fertility near replacement would raise standards of living (when factoring in the effects of age structure on families); and fertility below replacement would maximize per capita consumption (so long as the cost of providing capital for a growing labor force is included). Age structure and dependency ratios, for example, affect the outcome. Such analyses should be welcome in the policy world: many policymakers recognize that lack of data creates serious obstacles to effective policy (e.g. Takayama and Werding 2011). In sum, fertility and family patterns are influenced both by current costs and benefits, and by deep-seated influences that may derail the best-designed policies that affect current costs and benefits. Since Tinbergen (1963), in biology we call these current utility and phylogenetic or evolutionary influences. Human evolutionary demography is uniquely positioned to make a positive substantive difference in the real world. It sets what we learn in a context both broad and deep: the patterns we are uncovering give a rich context to what might once have been thought of as patterns peculiar to humans.

Human evolutionary demography adds enormous depth of information about life history patterns and ecological influences. It sets human data in the broadest context, creating important connections to evolutionary anthropology, demography, life history theory and behavioural ecology. It lets us examine what influences fertility patterns both broadly and in detail, at multiple levels and in a manner consistent with what we know about other species. If we want to influence fertility, for example, understanding how it is shaped by ecological or evolutionary patterns is crucial. Human evolutionary demography is a true, and important, nexus.

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<sup>1</sup> Note this chapter has been posted on the Open Science Framework website since 01/07/2019, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

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