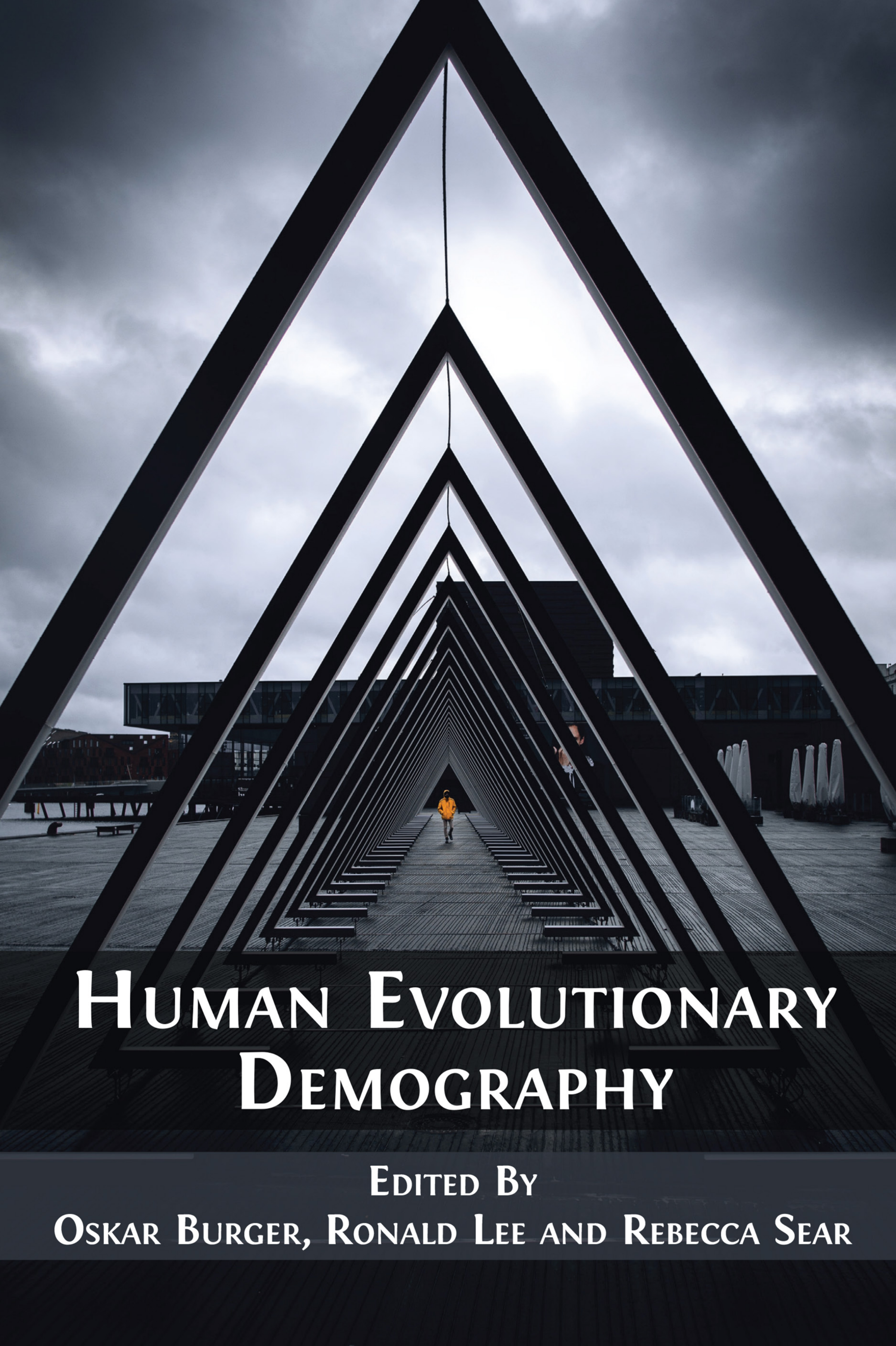

HUMAN EVOLUTIONARY DEMOGRAPHY

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22. A Theory of Culture for Evolutionary Demography

Heidi Colleran

Evolutionary demography is a community of researchers in a range of different disciplines who agree that "nothing in evolution makes sense except in the light of demography" (Carey and Vaupel 2005). My focus here is a subset of this research (henceforth "evolutionary demography" or "evolutionary anthropology") that originated in anthropology in the late 1970s and which typically examines micro-level phenomena concerning reproductive decision-making and the evolutionary processes generating observed patterns in reproductive variation. Scholars in this area tend to be more involved in long-term anthropological fieldwork than any other area of the evolutionary sciences. But card-carrying anthropologists are declining among their number as researchers increasingly come from other backgrounds in the biological and social sciences, with an associated decline in the contribution of ethnographic work. Most practitioners identify with the sub-field of human behavioural ecology — the application of sociobiological principles to human behaviour — and distinguish themselves from the sister fields of evolutionary psychology and cultural evolution. Human behavioural ecology has been criticized for abstracting away the details of both culture and psychology in its focus on adaptive explanations of reproductive behaviour, and for its commitment to ultimate over proximate causation. This chapter explores these critiques. Inspired by E. A. Hammel's seminal paper "A theory of culture for demography" (Hammel 1990), I examine how the culture concept is used in evolutionary research. Like Hammel, I argue that a theory of culture for evolutionary demography requires engaging more seriously with (and in) ethnographic work. I highlight some challenging examples to motivate discussion about adaptive reproduction and natural fertility. Going further, I advocate for cultural evolution as an integrative framework for bringing both culture and psychology into the core of evolutionary demography research. This will involve expanding our theoretical and conceptual toolkits: (1) building and testing proximate mechanistic models, (2) delineating and evaluating causal claims at multiple levels of analysis and time scales, and (3) exploring co-evolution or feedback between demography and culture.

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Why Has Culture Not Been a Central Concern in Evolutionary Anthropology?

Following the publication of E. O. Wilson's *Sociobiology* (Wilson 1975), and the "wars" that ensued (Segerstråle 2000), three streams of research on the evolution of human behaviour emerged: evolutionary psychology, human behavioural ecology and cultural evolution (Laland and Brown 2002). Of these, human behavioural ecology emerged directly out of socio-cultural anthropology (Borgerhoff Mulder and Schacht 2012). Working mainly at the micro-level these researchers were interested in the demography of underrepresented small-scale populations living in marginal environments (Howell 2000; Blurton Jones 1986; Borgerhoff Mulder 2000; Mace 1996, 1993; Chagnon 1979; Kaplan 1996; Hurtado and Hill 1996; Marlowe 2010; see Sear and others 2016b; Kennett and Winterhalder 2006; Kramer and Boone 2002). A principal concern was how the social and physical aspects of life in different ecologies affect the ability of individuals and their genetic lineages to maximize reproductive success (i.e. contribute genetic material to future generations). Key to the approach was the idea that we could learn about the evolutionary history of our species by studying populations living in conditions and pursuing life-ways that may closely approximate those of our ancestors.

Today, many evolutionary anthropologists work more often with comparative and large-scale databases than with primary anthropological data, and many identify as evolutionary demographers, but their concerns about adaptive reproductive behaviour are largely the same (Nettle and others 2013; Sear and others 2016a; Mattison and Sear 2016). In a globalizing world, practitioners now routinely explore reproductive behaviour beyond small-scale societies, and questions and methods are shifting. Statistical and formal models are becoming more sophisticated. Cross-cultural and macro-level studies are becoming relatively common (see for example Borgerhoff Mulder and others 2009, 2019), detailed case studies more rare. Applied and policy-oriented research is gathering steam (Gibson and Lawson 2014; Tucker 2007). Much work has crystallized around explaining global fertility decline, in response to Vining's clarion call that it is the "*central theoretical problem of human sociobiology*" (Vining 1986). Increasingly there are calls for more emphasis on "modernizing" or "modern" populations, meaning societies that have experienced the demographic and epidemiological transitions and which now exhibit low fertility and mortality rates (Mattison and Sear 2016 though see; Borgerhoff Mulder 2013 for an alternative view).

Many of our socio-cultural anthropology colleagues would deny that evolutionary demography so practiced even resembles anthropology (Ingold 2007). First, the field originated out of and remains based on applications of animal and economic models to reproductive behaviour (Cronk 1991) and has little time for non-evolutionary approaches within anthropology. Second, it involves a strong individualism, both methodological, in the sense that explanatory models take individuals as the unit of analysis, and ontological, in the sense that higher-level social phenomena are taken to be aggregations of individual level properties (they are typically not viewed as "social facts" in and of themselves). Third, the field maintains a fairly sharp distinction between proximate and ultimate explanations (Nettle and others 2013; though see Borgerhoff Mulder 2013) that foregrounds the fitness benefits of behaviour and brackets out (suspends judgment about) cultural processes. Many see this as downgrading cultural life — the very object of much anthropological enquiry — to a secondary or less causally interesting role, and it has made for an uneasy relationship with socio-cultural anthropologists, who do not recognize themselves in these commitments (Sahlins 1976; Ingold 2007; reviewed in Colleran and Mace 2011).

The reasons for the lack of culture, so to speak, are partly sociological: establishing human behavioural ecology as a respectable quantitative field of enquiry meant side-lining or subsuming culture for much of its early development (see Laland and Brown 2002 for review). Face-offs with evolutionary psychologists — who argued that contemporary human behaviour is adapted to Pleistocene conditions, and therefore cannot be considered adaptive today — meant that practitioners were initially concerned with defending the study of adaptive behaviour at all (Smith and others 2001; for recent review, see Stulp and others 2016). In contrast to evolutionary psychology's typical focus on universal characteristics of human psychology, behavioural ecologists showed that demographically relevant behaviour varies: between individuals and populations, across subsistence economies and over time, in adaptive ways related to fundamental energetic and other trade-offs (Kaplan 1994; Turke 1989; Hurtado and Hill 1996; Lawson and Borgerhoff Mulder 2016; Mace 2000; Cronk and others 2000).

But there are also profound theoretical reasons. The field draws on and develops life-history theory (Stearns 1989; Kaplan 1994; Charnov 1993), evolutionary game theory, and other theoretical approaches developed beyond anthropology, and a rational-actor approach to human decision-making — similar but not equivalent to that in economics and demography (Robinson 1997; Becker and Lewis 1973) — has become a central explanatory device. As in other fields, rational choice does not necessarily imply conscious reproductive strategizing, only that the pursuit of *proximate* aims such as status striving, wealth accumulation, social desirability, or any number of other cultural features, correlates with reproductive success, which is assumed to have been true for most of human history. A second claim in this field is that individuals come pre-loaded with *reaction norms* that evolved over long evolutionary time-scales: these refer to the genetically encoded range of responses an individual can express in a set of environmental conditions. This range, in theory, enables behaviour to remain consistent with fitness maximization (though see Baldini 2015).

The combination of a black-boxing of reproductive decision-making (henceforth the "rational-reproducer" model) and a kind of ecological relativism (meaning that you cannot fully understand particular reproductive outcomes outside of the particular ecological conditions they occur in) has been extremely successful (Nettle and others 2013; Sear 2015b). But this orientation leaves two deep questions about human reproduction unexplored. How does culture actually contribute to demographic outcomes? And what does the psychology of reproduction look like? Evolutionary anthropologists have been asking themselves these questions for a while (Borgerhoff Mulder 2013; Mace 2014; Roth 2004), but a clear way forward has not been articulated (see Colleran 2016 for a recent attempt).

Culture in Demography: The Emergence of Anthropological Demography

Demography and anthropology go back a long way and many foundational anthropologists were acute observers of demographic patterns. But demographers and socio-cultural anthropologists have come to distrust each other's methods and insights over time (Scheper-Hughes 1997; Randall and Koppenhaver 2004; see Roth 2004; Colleran and Mace 2011 for comparison with evolutionary anthropology). Socio-cultural anthropologists have long critiqued the limited role given to culture in demographic research, and the lack of qualitative and interpretive analysis to draw out the dimensions of social life that are not measurable using quantitative survey instruments and population level analysis (Price and Hawkins 2007; Greenhalgh 1990; Hammel 1990; Hammel and Howell 1987; Cleland and Wilson 1987; Pollak and Watkins 1993; Behrman and others 2002; Hirschman 1994; Fricke 1990; Randall and Koppenhaver 2004; Scheper-Hughes 1997). A seminal paper in this literature is Hammel's "A theory of culture for demography" (Hammel 1990), the title of which I adapt only slightly for the current chapter. Hammel (1990) described the use of "culture" as "mired in structural-functional concepts that are about 40 years old, hardening rapidly, and showing every sign of fossilization" (p. 456). He argued that the study of demographic behaviour has actually been hampered by the widespread use of "culture" in different inappropriate guises and advocated a much greater use of fine-grained studies and ethnography. He also emphasized the importance of feedback over both the short- and long-term: culture shapes behaviour, actors redefine culture, behaviour shapes cultural change.

These concerns led to the development of the sub-field of anthropological demography (Kertzer 2005; Bernardi and Hutter 2007; Basu and others 1998; Fricke 1997), which examines the complexities of demographically relevant behaviour and the attitudes, perceptions, concerns and anxieties associated with it. Anthropological demographers call into question the methods and classifications used to define culture and other foundational analytical constructs in demographic data collection; they reject the decontextualized rational-actor model inherent in most demographic research, and they critique the causal assumptions (and lack of feedback) in demographic models. The field now draws widely on research that is often only tangentially connected to demography: anthropological studies of menstruation, pregnancy and childbirth, contraceptive choice, access and use, new reproductive technologies, infertility, HIV and the spread of STIs, migration, mortality, development, and many other topics besides. Their focus is on how society, politics and culture shape the biological experiences of birth, death and migration (e.g. Kreager 2017; Pooley and Qureshi 2016; Kanaaneh 2002; Johnson-Hanks 2007; Bharadwaj 2016; Caldwell and Caldwell 1987; Scheper-Hughes 1993).

Anthropological demographers have directly engaged in critiques of demographic practice, and their methodological influence has been substantial. Anthropological methods such as focus groups or open-ended interviews are now regularly used in "mixed-methods" studies and to design better quantitative data collection instruments (Randall and Koppenhaver 2004; Basu and others 1998). Basic analytical categories such as "household", "traditional versus modern", "reproductive decisions" and concepts such as "ideal family size", "natural fertility" and "insurance effects", all central to large-scale demographic data collection and analysis, have been given more nuanced treatment, even revised, following the critical interventions of anthropological demographers (Randall and others 2011; LeGrand and others 2003; Bledsoe and others 1994; Randall and LeGrand 2003; Johnson-Hanks 2002; Johnson-Hanks 2005; Olaleye 1993; Randall and Coast 2015). Others have shown that the way demographic data is collected affects the data that gets produced in many ways, from underrepresenting vulnerable populations through survey definitions (Randall and Coast 2015) to misinterpreting what cannot be talked about for lack of knowledge or interest (Randall and Koppenhaver 2004). Despite this impressive impact for such a small field of enquiry, the theoretical contributions of anthropological demographers still remain on the fringes of mainstream demography (Bernardi and Hutter 2007; Johnson-Hanks 2007). Many socio-cultural anthropologists have given up on collaboration with quantitative researchers at all (Scheper-Hughes 1997). While evolutionary anthropologists regularly cite the work of anthropological demographers, sadly, the reverse is not true: they have long viewed the evolutionary work as “thoroughly teleological” (Hammel and Friou 1997 cited in; Roth 2004).

Cultural Evolution as a Unifying Framework

The prospects for integrating both culture and psychology into evolutionary demography are more promising now than they ever were. The main reason is that the field of cultural evolution (or dual inheritance theory) — the third of the research streams that emerged after the sociobiology wars — has developed into a multidisciplinary field that quantitatively studies both the transmission of culture and the population level dynamics of norm psychology (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). Cultural evolution has ushered in a major change in our orientation to human evolution: our evolved psychological capacities themselves arose out of a long history of learning from and living with others and these social learning skills — in addition to the cost-benefit calculations of human behavioural ecology — have allowed interacting groups of people to produce cultural innovations that may have radically altered aspects of our physiology, anatomy, and psychology in crucial ways (Henrich 2016). While these cultural transmission mechanisms (or learning biases) evolved to help individuals acquire adaptive behaviour, allowing rapid calibration to the environment, the two inheritance channels (culture and genetics) can become decoupled, or even generate conflicting pressures (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981).

The crucial innovation by these researchers was to formalize a set of quantitative tools for analysing and modelling the dynamics of culture. Contemporary cultural evolutionary research is expansive, incorporating processes of cultural selection, mutation/innovation, drift and migration (Mesoudi 2011), niche construction (Odling-Smee and others 2003) — whereby individuals modify the environments they live in, affecting the selection pressures they are subject to, and thereby creating feedback in the evolutionary process — and other non-genetic inheritance channels (Jablonka and Lamb 2005), cognitive and symbolic evolution (Sperber 1996) and cyclical processes of change (Turchin and Nefedov 2009). The field draws on population-genetic and epidemiological diffusion models (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985) to examine change in the frequencies of cultural traits over time; models and experiments of social learning and cognition to understand how individual characteristics give rise to population level distributions of cultural traits (Henrich and Boyd 1998; Henrich and others 2005); and macro-evolutionary and phylogenetic studies of societies and languages (Mace and Holden 2005; Jordan and others 2009; Mace and Pagel 1994) to make explicit the path-dependent histories of culture as well as identifying sources of shared ancestry. Cultural evolution is now a thriving multidisciplinary arena for experimental, observational and quantitative work at multiple levels of analysis.

Cultural evolutionary theory and human behavioural ecology have led a parallel existence for most of their development because of a range of different starting assumptions and overlapping conceptual categories (Borgerhoff Mulder 1998; Colleran 2016). Cultural evolutionists have also had their disagreements with evolutionary psychologists, who have tended to consider that culture is "evoked" by fitness-relevant environmental experiences (Barkow and others 1992), and not "transmitted" through learning and interaction and therefore separable from fitness constraints. Increasingly though, ideas from cultural evolution are percolating into evolutionary demography (for review see Colleran 2016). The combination of genetics-style "population thinking" with social psychology-inspired behavioural models in cultural evolutionary theory broadens the methodological and theoretical landscape for evolutionary demography beyond optimality and rational-reproducer models. As an overarching framework, cultural evolution holds great promise for bridging some of the gaps between what socio-cultural anthropologists and evolutionists care about, namely, a focus on the socially constructed nature of human cultural systems on the one hand, and a commitment to using model-based, quantitative methods to develop evolutionary theory on the other. It does this through providing quantifiable connections between individual decision-making, observation and learning, information flow in (structured) populations and group level cooperation and competition.

But this expanded set of theoretical tools comes with a need to relax the often sharp distinction made by behavioural ecologists between proximate and ultimate (i.e. functional) explanations (Nettle and others 2013; see, for example Borgerhoff Mulder 2013; Laland and others 2011), as well as a much more thorough incorporation of individual differences in cultural evolutionary theory. It also comes with a need for much more ethnography, and greater rapprochement with socio-cultural approaches to demography. The fields of evolutionary demography, cultural evolution and anthropological demography have largely ignored each other over the years, but have much to gain from greater communication. In the rest of this chapter, I discuss the gaps and overlaps between them. This involves discussion of assumptions related to the culture concept, reproductive decision-making, natural fertility, maladaptive reproductive behaviour, and proximate/ultimate causality.

The Culture Concept in Evolutionary Demography and Cultural Evolution

Hammel (Hammel 1990) described two major tendencies in demographic theorizing about reproduction: "sociological" approaches that tend to underplay individual agency through homogenizing culture-concepts, and "economistic" approaches which tend to universalize individual rationality, giving complete agency to individuals. This distinction captures well the stereotypical critiques made against cultural evolution and human behavioural ecology, respectively, but in reality both fields make use of these tendencies in different ways and so cannot be summarized under this simple typology.

An example of a sociological use of culture is the *culture-as-identifier* approach to describing social phenomena (e.g. the French fertility decline, high-fertility among Irish

Catholics). Cross-cultural evolutionary research makes frequent use of such high level population descriptors such as subsistence type, religious or ethno-linguistic groupings (Sellen and Mace 1997; Bentley and others 1993; Mace and others 2005; Henrich and others 2006) which can act as a stand-in for "culture". In this formulation, all that culture does is effectively label a particular demographic pattern in time and space. While it does often identify something about a particular collectivity that we seem to readily imagine as "cultural", the designation is merely descriptive and does not advance any theoretical claim about why that cultural group behaves in the way it does. Culture here is doing descriptive or classificatory work, not explanatory work. Some human behavioural ecologists have directly criticized this approach in cultural evolution by highlighting that behaviour can be just as varied within a particular collectivity as it is between them (Lamba and Mace 2011). However, much the same critique could be levelled at other common descriptors used frequently in demographic research, such as "educated", which indicates, through membership of a particular category, a person's likely reproductive behaviour (i.e. that they may have lower fertility than their less-educated peers), but says nothing substantive about why their behaviour is different. This formulation does not involve a theory of social action, or any theoretical claims about the transmission, acquisition or negotiation of either culture or demographic behaviour.

Comparisons can of course be finer grained, such as those in multi-community settings within the same ethno-linguistic groups (Colleran and others 2015, 2014; Alvergne and Lummaa 2014). This approach appeals to *culture-as-context*, a form of natural experiment where the effects of some cultural features can be to some extent isolated from the broader cultural milieu. Contextual approaches are becoming widespread in demography, and are increasingly used to disentangle the levels of aggregation at which a purported variable has causal power (Kravdal 2002, 2012; Stephenson and others 2008). This represents a more nuanced treatment of the culture-as-identifier approach, especially where there is explicit measurement of proxy variables at different levels of social organization. However, when used without any mechanistic links between different levels of analysis, such as social network connections, this approach suffers from similar limitations to the approach above.

Other lines of research compare reproductive outcomes among communities with similar economic, cultural or ecological backgrounds but which nonetheless have distinctive institutional or socio-cultural features such as inheritance or marriage systems (Leonetti and others 2007; Gibson and Sear 2010; Gibson and Gurmu 2011; Holden and Mace 2003; Mace and others 2003). This characterizes culture as the playing out of a set of largely autonomous rules or institutions, such as kinship or social stratification. This is *culture-as-structure*, and implies that social action responds to pre-set and exogenous structures of organization. Under this model demographic change is simply the outcome of individual responses to infrastructural or institutional change, but we do not learn why or how those structures themselves evolve. Instead, structures, rules and institutions are being continuously rebelled against, reinterpreted, reformed and updated through individual and collective actions. In the jargon of evolutionary theory, institutions and social structures coevolve with changes in population, ecology and economics.

A fourth approach is *culture-as-ideology*. Take, for example, the ways that reproduction is moralized in every population. People are often aware of the "right" levels and rates of reproduction in their particular environment, the right parenting strategies. Individuals can easily point to others who have had too many or too few children according to their social or cultural context. We see these unspoken rules everywhere. One way to think about this is to consider reproduction as a form of collective good (Kohler 2000), since the resources of the local environment are needed to jointly produce the children of multiple co-resident families, lineages and others. Indeed the "cooperative breeding" model of human evolution does precisely this (Hrdy 2007), and a relatively large literature now shows that conflict and cooperation with kin is an important factor in women's reproductive outcomes (Sear and Mace 2008). As part of this, an evolved ability to internalize the social norms of a particular group is likely to facilitate this kind of cooperation (Gavrilets and Richerson 2017). Coordination on locally adaptive social norms that regulate appropriate reproduction can be achieved via the sanctioning of norm violators (Fehr and Gächter 2002). Ideologies of reproduction could be shaped by kin interactions and interests that themselves structure the costs and benefits of particular reproductive actions — what Leonetti has called "kinship ecologies" (Leonetti 2008). These can themselves vary according to structural-cultural features — lineality (Pollet and others 2009) or inheritance system (Gibson and Sear 2010) — but they are also affected by macro-level cultural and economic changes that alter social network structures, which can determine how prominent or influential kin are in the reproductive lives of women (Newson 2009; Newson and Postmes 2005; Colleran 2020).

The strong emphasis on individual costs and benefits to reproduction in human behavioural ecology means that the culture concept is not well-developed beyond the idea that it forms part of the "socio-ecology" (Cronk 1995). This phrasing is a nod to the fact that culture is important in the determination of reproductive outcomes, but it is thought to be just one element among the set of "proximate" determinants of demographically relevant behaviour that are often, though not always, a secondary concern (Nettle and others 2013). This is a form of economistic approach that gives a large amount of agency to individuals to figure out the best reproductive strategy under a given set of circumstances (the rational-reproducer). In fact, for many evolutionary demographers, the success of a cultural trait itself will often be associated with its ability to confer fitness benefits on individuals, for example a marriage rule that delays marriage for men, which, by separating reproductive generations of women, adaptively reduces reproductive competition between them (Alvergne and Mace 2012). This is *culture-as-adaptation*: cultural traits are themselves adaptations that help populations optimize their reproductive success. Both human behavioural ecology and cultural evolution make use of this kind of conceptualization.

Adaptive Culture?

However, the causal claim here is a strong one: it says that because culture itself evolved to help us acquire adaptive behaviour, the genetic program is ultimately in charge. If a cultural mechanism is maladaptive (reducing fitness over time), then natural selection should logically weed it out of the broader population, since those individuals and groups that practice it will eventually be out-reproduced by those that do not. This idea that cultural adaptations have primarily functional benefits remains closer to classic ecological and materialist anthropology and archaeology (Harris 2001) than to contemporary socio-cultural streams in anthropology, and is exemplified in its extreme form by E.O. Wilsons claim that:

> The genes hold *culture* on a *leash*. The *leash* is very long, but inevitably values will be constrained in accordance with their effects in the human gene pool (Wilson 1975).

Human behavioural ecologists have traditionally subscribed to this interpretation, often implicitly if not always explicitly. Indeed the concept of "adaptive lag" — the idea that when humans adapt slowly to changing environments there will be a period of suboptimal behaviour — and which is often appealed to regarding fertility decline, is a logical conclusion of this view of culture (Laland and Brown 2006). Cultural evolutionary research differs on this point, in three ways.

First, for cultural evolutionists the success or fitness of a particular cultural trait is not as strongly tied to assumptions about fitness maximization, and is instead inferred from frequency changes of a trait in the population over time, assuming certain learning-rules or structures. Much cultural evolutionary theory is not strongly committed to strictly Darwinian or selectionist approaches (Lewens 2015). This means that other non-adaptive processes can drive the spread of a particular cultural trait in a population. Crucially, it allows for the spread of explicitly genetically maladaptive traits. This logic is the basis for most cultural evolutionary work on fertility decline (Colleran 2016). This more permissive version of cultural evolution is one that Lewens (Lewens 2015) has described as "kinetic" (broadly, non-selectionist) and which is often broad enough to encompass many different kinds of change over time. An advantage of this is that it can potentially connect with more socio-cultural approaches to demographic change that do not focus on adaptive functions of behaviour.

Second, the fact that humans are continually interacting with, modifying and sometimes constructing their socio-ecological environments means that evolutionary pressures themselves are also constantly evolving (Laland and Brown 2006; Odling-Smee and others 2003). This appreciation of the centrality of feedback in the evolutionary process is a hallmark of the "niche construction" perspective. A niche construction approach, within the broader framework of cultural evolution, has implications for how we expect individuals and communities to adapt to and change their socio-ecologies on short to medium time scales, thus removing the need to appeal to adaptive lags and temporarily suboptimal behaviour (Laland and Brown 2006). Again, this orientation to the evolutionary process makes connections with socio-cultural anthropology, by allowing the participatory character of cultural life to be more explicitly framed in evolutionary terms.

Third, some cultural evolutionary models assess the fitness of a cultural trait in terms of its function at the group (or institutional) level rather than at the individual level. Because culture comes in packages of institutions, norms, beliefs and practices, some elements of which can be adaptive, they can have many different effects: reducing interaction costs in social networks or brokering cooperation, generating regularity in behaviour though institutions, norms and sanctioning, or entrenching power-relations and divisions of labour. A cultural trait that causes some groups or institutions to spread at the expense of others, via population growth, expansion, migration or other means of cultural prestige or soft power can in principle spread by between-group cultural selection (Richerson and others 2014).

In theory individually costly behaviours can spread in a meta-population if the aggregate outcome is beneficial to the group (Boyd and Richerson 2002). Again, fertility decline is a good example where this logic could be applied. Historical fertility declines during the Industrial Revolution are thought to have been generated through feedback between population density and technological innovation, which spurred economic growth (Galor 2011). The interconnectedness of contemporary nation states through labour and migration transfers, innovation and capital, has increased the levels of interdependence between groups in international trade and supply networks to an unprecedented level. Technologically advanced countries appear to be able to effectively down-regulate each other's fertility rates through competition and cooperation for increased economic productivity (Dang and Bauch 2010). Fertility reductions can drive temporary rises in the rates of economic growth by altering age structures and the amount of people available to take part in wage labour, a phenomenon known as a "demographic dividend" (Bloom and others 2003). When considered in a multilevel framework, demographic benefits at one level of aggregation can trade off against costs at another.

Individual Differences

If evolutionary demography tends to focus overly on individual differences, then cultural evolutionary theorizing tends to undervalue them, by rarely including individual resource constraints on reproductive options. Instead, cultural evolutionary models relevant to demographic behaviour have tended to assume that individuals are undifferentiated with respect to their opportunities to access information, can perfectly sample from cultural learning models and are free to enact their reproductive preferences (reviewed in Colleran 2016). Having said that, empirical experimental studies in cultural evolution are much more focused on individual variation and on the selective use of social learning strategies dependent on a wide range of constraints and incentives (Mesoudi and others 2016; Kendal and others 2018), so this difference between theory and empirical strategy is unlikely to last for long.

While cultural evolution is now a broad school of thought incorporating the evolution of socially transmitted information, technologies, norms and institutions, the culture concept most widely used is broadly "ideational" or "informational": *culture-as-information*. This definition conceptually fuses information transmission with behaviour (culture is information capable of affecting behaviour that is transmitted socially (Boyd and Richerson 1985)), and the innovation-diffusion models typical of cultural evolutionary research usually assume a tight relationship between information flow and behavioural expression (Henrich 2001). This formulation is very close to the ideational models prevalent in demography (Cleland and Wilson 1987) which are also often modelled using diffusion dynamics (Casterline 2001; Rogers 2010). Is this tight link between information diffusion and behaviour justified? In theory, the frequency of a cultural trait (say, a belief about the value of having fewer children) within a specific group should not only influence the chances that an individual adopts the trait, but also the chances that it is translated into behaviour (actions consistent with having fewer children), and there is some social psychology evidence suggesting that feedback between individual and group "norms" may have this effect (Smith and Louis 2008). But the process by which transmission of social information is translated into actual behaviour has not been a focus for cultural evolutionary theory. Indeed there is plenty of evidence that people say one thing and do another, that subjective intentions do not predict behaviour (Armitage and Conner 2001; Ní Bhrolcháin and Beaujouan 2019) and this is an anthropological truism: the distinction between ideal and real culture. Some models in cultural evolution take this partly into account by allowing individuals to vary in their propensities to adopt particular behaviours and/or by allowing behaviours to be probabilistically adopted (Kandler and Steele 2009; Kendal and others 2005). Nonetheless, diffusion dynamics of the type typically examined in cultural evolution are known to be sensitive to individual variation, for example in wealth and income heterogeneity (Kandler and Steele 2009) and population sub-structure (Laland and Kendal 2003). A greater focus on how these effects may influence cultural evolutionary dynamics, as well as empirical tests of these hypotheses are needed.

Cultural evolutionary theory has been at the forefront of modelling how demographic properties such as population size or connectivity crucially affect the accumulation and loss of culture over time (Henrich 2004; Powell and others 2009). There has been much less focus on how culture might affect demography. Many early ecological anthropologists (the researchers most similar to much contemporary evolutionary anthropology), aimed to show that the demographics of small-scale populations were culturally regulated, through ritualized warfare (Rappaport 1984), culturally determined age-structures (Roth 2004), or other forms of cultural equilibrium that maintained a balance between population growth and carrying capacity (Harris 2001). The question of cultural population regulation is an old one in anthropology and there are countless examples in the ethnographic literature of cultural institutions, rules, taboos, rituals and practices affecting reproductive opportunities (Hammel and Friou 1997). This angle has been neglected by both cultural evolution and evolutionary anthropology, but is one which anthropological demographers would have much to say about.

Proximate and Ultimate Causality: A Distinction that Hampers More than it Helps?

Following Tinbergen's delineation of four different "why" questions in evolutionary analysis (proximate, developmental, ontogenetic and ultimate) and Mayr's distinction between proximate and ultimate explanations (Tinbergen 2010; Mayr 1961; though see Laland and others 2011), evolutionary demographers often expect different kinds of explanation to be mutually consistent and enriching (see Colleran and Mace 2011 for an overview). Nonetheless, they do assign distinct causal powers to different kinds of explanation. Proximate mechanisms, for example, do not have the causal power to fundamentally de-rail the ultimate motivations that humans were endowed with over millennia of evolution. Where they do exhibit mismatch, this will be a temporary state of affairs (adaptive lag), and will most likely be corrected over the long term. Evolutionary demographers agree that zooming in on the cultural nuances of a particular behaviour in a particular context will undoubtedly reveal interesting details about the local perception of costs and benefits, as well as the various meanings associated with reproductive activities. Some, but by no means the majority, give ethnographic details in their publications. Still, the majority of practitioners defend the benefit of abstracting away from these details to get at the underlying long-run evolutionary logic. When faced with the criticism that culture seems undervalued in their research, evolutionary anthropologists often point out that culture is conceptually already in the models: culture is part of the socio-ecology. This conceptual move, to incorporate proximate cultural mechanisms into the very definition of adaptive behaviour, allows the practitioner to avoid having to define culture at all. This makes the socio-ecology a slippery concept to work with; because it is unclear which parts of culture contribute to adaptive reproduction, and which ones do not.

Much the same can be said about the concept of natural fertility. Originating in the 1950s work of the demographer Louis Henry (Henry 1961; later Coale 1971), natural fertility refers to the age-specific pattern of fertility that is assumed to emerge in the absence of deliberate control of the number of children being born. If there is no *parity-specific stopping* in a population (indicating that people stopped having children after a certain desired family size was reached), natural fertility should result in a pattern of regular birth intervals. Both physiological and cultural constraints can generate this baseline pattern: fertility can be naturally limited by anything from nutritional status to breast-feeding practices, from marriage-rules to post-partum sexual taboos. This means that while the level of natural fertility (the number of children born/surviving) can vary dramatically across cultures (Bentley and others 1994), we should still be able to judge a natural fertility population from the age-specific pattern of reproduction. In practice, many researchers do not use age-specific fertility profiles to determine if their study populations are experiencing natural fertility: more often, the absence of significant modern contraceptive use is the proxy.

The distinction between natural and controlled fertility turns less on the difference between physiological versus cultural determinants of reproduction, and more on the idea of conscious or planned behaviour versus unconscious or unplanned behaviour. In the famous words of the demographer Ansley Coale, reproductive decision-making can be more or less part of a "calculus of conscious choice"(Coale 1973). Viewed in this light, a lack of parity-specific stopping coupled with compliance with strong reproductive norms can be taken as evidence of unconscious (and therefore natural) fertility, even where cultural norms end up lowering overall fertility rates. Parity-specific stopping, on the contrary, is almost always thought to be conscious and, implicitly (though this is unclear), to a large extent outside the realm of cultural norms. It is important to note that no human population exhibits maximal biological reproductive output: cultural and other constrains are everywhere in operation (Lawson and Borgerhoff Mulder 2016).

Even with the conceptual de-emphasis on cultural determinants in favour of a form of deliberative decision-making, the natural/controlled distinction is hard to justify in real-world populations (Bledsoe and others 1994; Johnson-Hanks 2002; Caldwell and Caldwell 2003; Bledsoe 1996). There is clear evidence that: (1) regular patterns of birth spacing typical of natural fertility profiles can be generated as much by the deliberate use of modern contraceptives as by a lack of them, in line with locally appropriate spacing norms (Bledsoe and others 1994); (2) women's perceptions of what counts as "modern" contraception are culturally inflected, often leading them to use methods of fertility control that are not typically counted in large-scale surveys (Johnson-Hanks 2002; Colleran and Mace 2015), and (3) the majority of twentieth-century fertility declines are more likely to have been driven by reproductive strategies that are not dependent on the number of children already born (Daniel J. Hruschka and others 2018).

Natural fertility ultimately raises more questions than it answers, because casting such a wide net over the causal structure of reproductive behaviour does not help to delineate causal theories about that behaviour. To a large extent, the same is true for the socio-ecology. Evolutionary demographers have repeatedly staked out research territory through their focus on ultimate explanation and there can be no doubt that this has been fertile ground (Stulp and others 2016; Nettle and others 2013; Sear 2015a; Colleran and Mace 2011). Nonetheless, it is the motivations and perceptions that tell us not only what is locally interesting about reproductive behaviour, but in many cases, what is important for a causal understanding of it. Simplified models are necessary for an evolutionary understanding of behaviour in the broadest sense, but they are not sufficient to explain why reproduction varies the way it does empirically. Proximate explanations are not just "how" explanations, they are also often "why" explanations (Borgerhoff Mulder 2013).

Do We Have a Comprehensive Theory of Reproductive Decision-making?

There is much talk of "reproductive decision-making" in evolutionary demography. Mostly this amounts to a reductive but extremely widely applicable rational-reproducer model focused on how people integrate over the various costs and benefits of particular reproductive activities to optimize reproductive success. It is not a requirement that such "decisions" are conscious, nor even that they are psychological — they can be "taken by a woman's physiology" (Sear and others 2016a) where, for example, energetic conditions preclude conception. While intended to be integrative in much the same way that socio-ecologies are integrative of biological and cultural mechanisms, it is doubtful whether any practicing evolutionary anthropologist thinks this is a comprehensive theory of reproductive decision-making. Anthropological demographers have strongly criticized this decontextualized approach in demography for not taking into account how culture structures the opportunities for reproduction, since both the extent to which "costs" or "benefits" are interpreted as such, and the actual values they refer to, vary substantially across contexts (Cleland and Wilson 1987; Lesthaeghe 1980; Pollak and Watkins 1993; Sahlins 1976). Socio-cultural anthropology has largely abandoned any attempt to make pan-human psychological claims in favour of understanding culture-specific rationalities. These are the cultural lenses through which all behaviour is interpreted, reflected upon, incentivized and challenged.

Very little evolutionary work has focused on the actual psychology of reproduction, let alone how culture subtly or overtly influences the perception and selection of reproductive choices. To the extent that there is research on the psychological mechanisms underlying fertility decision-making, it is fragmented and based mainly on research with WEIRD populations: Western, educated, industrialised, rich and demographic (McAllister and others 2016; Henrich and others 2010).

In demography, the now-large literature on "ideal fertility" has tried to address some aspects of the gap between planned and unplanned fertility, by focusing on the "unmet need" of women for modern contraception (Casterline and Sinding 2000). This refers to the difference between the number of children women say they want and the number of children they actually give birth to. Other frameworks such as the theory of planned behaviour have been incorporated into demography as a way to capture the connections between intentions and behaviour, though not without question (Bachrach and Morgan 2011). Again, there is substantial evidence that these formulations may be insufficient: people often do not have clear reproductive goals, are inconsistent or ambivalent when it comes to enacting the preferences they report to researchers, and indeed often construct their ideal family size as they go through their reproductive lives (reviewed in Ní Bhrolcháin and Beaujouan 2019; see also Mason 1992). Opportunistic rather than deliberative reproductive decisions seem common (Randall and LeGrand 2003; Johnson-Hanks 2005). Much more basic research in this area is needed. Cultural evolution can be useful, through its focus on the evolution and dynamics of norm psychology, as can more comprehensive theories of social action, such as the theory of conjunctural action emerging from anthropological demography (Johnson-Hanks and others 2011).

"Maladaptive" Cultures of Reproduction

The explanatory strategy of subsuming proximate mechanisms in order to focus on ultimate outcomes is easy to defend when proximate and ultimate explanations are consistent. It is much harder when they conflict. The most obvious example is the global transition to low fertility, which does not appear to optimize reproductive success (Colleran 2016; Borgerhoff Mulder 1998). Because of its global reach and seemingly law-like patterning, fertility decline is finally drawing the focus of evolutionary demographers to proximate mechanisms (Sear and others 2016b; Colleran 2016). But the ethnographic record offers a cornucopia of examples where the reproductive behaviour of "traditional populations" either does not align with a *prima facie* genetic program of fitness-maximization, or where practices explicitly designed to increase fertility have actually had the opposite effect (for review see Paul 2015).

A striking example involves the ritual practices of *otiv bombari* among the Marind-Anim of western Papua, Indonesia (Irian Jaya), which mandated that upon a woman's marriage or resumption of active village life after childbirth, she participate in sexual intercourse with all the men of her husband's sub-clan (often up to ten or more men) over the course of a single night. These practices were intended to promote fertility among other things, in line with a rich cosmology that required the collection of growth-promoting semen mixed with the vaginal fluid that follows ritualized sexual intercourse (Baal 1966; reviewed in Paul 2015; Knauft 1993).

In fact, the practice was implicated in abnormally high rates of chronic cervical inflammation among women, leading to widespread sterility and substantial depopulation as a result. The logic of fitness-maximization teaches us to expect this practice, or even this population, to eventually be lost through natural selection. But the Marind did not die out due to this "maladaptive" cultural mechanism, and until after the colonial encounter in the 1950s, neither did the practice. Depopulation was largely compensated for by the kidnapping of women and young children during expansionary raiding expeditions associated with head-hunting, and otherwise through adoption. It is estimated that up to 20% of the population was supplied in this way before pacification: once money came into the picture, available data show that up to 25% of children in some communities were purchased in the post-pacification period (Knauft 1993). These children were raised as full members of the Marind, often without the knowledge that they were from another ethno-linguistic group (Baal 1966).

The practice of collecting life-giving sexual fluid, through ritualized or serial sexual intercourse and/or wife sharing, was widespread across south coast New Guinea, parts of the highlands, and some other areas of Melanesia in the twentieth century (Knauft 1993). These were neither peripheral nor transient cultural practices and are an important theme linking widely differing linguistic and cultural groups in Melanesia. The Marind-Anim in particular were a highly demographically successful ethno-linguistic group, with an extended alliance system incorporating many neighbouring groups (and different language families). Internal relations were peaceful among some 16,000 persons and without any discernible hierarchical political structure, despite the fact that their cultural practices substantially influenced their demography and within-group genetic relatedness. The strategic use of adoption to bolster population declines is not unique to this group — in fact it is a feature of many other cultural groups around the world, too (Paul 2015).

It should be clear that paying attention to these cultural mechanisms reveals more than just some interesting details about how individuals might be interpreting their reproductive choices. The entire causal structure driving the maintenance of both a cultural practice (e.g. *otiv bombari*) and the ethno-cultural population that espouses it (the Marind) is brought to light by a deeper understanding of its internal cultural logic. Whether the individuals involved in this case were maximizing genetic output seems, if not irrelevant, then a problematic focus at best: lineages and groups were certainly being reproduced over time, but not necessarily via the production of genetic kin. As Paul (2015), in his treatment of the tensions between cultural and genetic inheritance, asks: "*by what right do we give the genetic [channel] preferential treatment in judging the whole system just described as 'maladaptive'?*" I would go further: if cultural practices like *otiv bombari* and ethno-demographic expansion are mutually reinforcing, why call any part of it maladaptive? And at what level (individual, group, institution) is it maladaptive? This example provokes us to think harder about the foundations of an evolutionary approach that claims that culture, broadly construed, is for calibrating individual behaviour to local ecologies in the service of reproductive success. The opposite scenario, where demographic activity (expansion, adoption, kidnapping) serves to ensure cultural continuity, is also clearly possible (Paul 2015). A co-evolutionary approach to demographic and cultural evolution that does not privilege one factor over another as being more causally forceful is needed.

All Cultures Are Cultures of Reproduction

We do not need to rely on examples in "natural fertility" contexts to see how culture influences reproduction in ways that alter demography at higher levels of aggregation. We can apply the same kind of thinking in a large-scale context. Consider contemporary western Germany, which has one of the lowest fertility rates in the world and some of the best maternity conditions, a public healthcare system and a high quality of life (among other things, a recent poll showed that Germans get more sleep than any other nation in Europe). And yet in western Germany a widespread stigma surrounds the return of women to the workplace after they become mothers, contributing to higher part-time and unemployment rates among childbearing women (especially highly educated ones) and to persistent gender pay-gaps and inequality in the workplace (Grönlund and Magnusson 2016). Women who do return to work may be pejoratively referred to as *Rabenmutter* ("raven mother"): a derogatory term has been used in Germany for centuries to describe women who abandon their children and are thus considered bad parents. This phenomenon is pervasive in western Germany, where a traditional male-breadwinner model of the family dominates, but not in eastern Germany which was part of the socialist DDR (German Democratic Republic). In the west, highly educated women are more likely to remain childless and less likely to have children outside of marriage than in the former East Germany, where women tend to start reproduction at an earlier age and more readily envisage being working mothers (Bernardi and Keim 2017). As recently as 2012, only 27% of the highest-educated western German women used day-care facilities, compared to over 70% in the former East Germany. Opinions differed dramatically, too: 32% of all western German women agreed that pre-school children suffer when their mothers return to work during this period and 42% thought that family members should do the childcare. In the former East only 13% agreed that children suffer in this way and only 17% agreed that family should take up the childcare (Schober and Stahl 2014).

These differences show how the experience of different political regimes and historical events can persist in the reproductive decision-making of women today. These underlying values, which developed over historical and not evolutionary time periods and which have a range of demographic effects, only make sense within a particular cultural context. This kind of path dependency often gets overlooked in evolutionary demography. While this example is obviously not about a socially mandated practice like *otiv bombari* among the Marind, and while the institutional and economic context is arguably more complex, the social stigma of being a *Rabenmutter* in (western) Germany is nonetheless great enough that it is keeping many qualified women out of the workforce. This taboo is also at work among career-minded women avoiding childbearing (Bernardi and Keim 2017), and is therefore at least partly implicated in the continuing shrinking of the population, the persistent gender inequality in the workplace and other economic and social impacts. And to stretch the analogy with the Marind, the downstream effects are also comparable. As Germany's "indigenous" population declines and its age structure becomes unbalanced, leaving fewer young people and women to work and raise taxes, the state has resorted to "importing" its workforce through unprecedented levels of mass migration. This situation is currently the topic of heated debate as Germans revisit questions about their cultural values and identity in a contemporary multicultural context.

Distinguishing Causality in Cultures of Reproduction

These examples are not meant to claim that culture alone determines reproduction. Rather they serve to complicate our picture of the relationship between culture and demographic outcomes, and highlight the fuzzy distinctions between natural and controlled fertility. Should the Marind-Anim be described as a natural fertility population, when their reproductive decisions so obviously involve highly planned kidnapping and adoption of persons from unrelated groups? Should evidence that highly autonomous Western German women are culturally incentivized — probably largely unconsciously — into "stopping" behaviour be considered part of the spectrum of natural fertility? Neither seems an appropriate description. Instead, the point I want to emphasize is that culture and demography co-evolve, sometimes to the benefit of a cultural entity (e.g. an ethno-linguistic group, institution or trait) and sometimes to the benefit of a demographic entity (e.g. an age-cohort or family lineage). Of course, such neat distinctions between cultural and demographic entities are not always going to be clear-cut, but this only further highlights the need for a co-evolutionary approach to addressing these questions.

But identifying causal mechanisms turns out to be harder in high fertility populations where cultural and genetic motivations may seem more in sync than in low fertility ones where the mismatch may be more obvious. This is a problem for our field because theories that are functionally equivalent (i.e. lead to equi-final outcomes) are not necessarily causally equivalent (Okasha 2006). Compare the following causal claims about the same hypothetical population:

> (1) Fertility is high because a history of political oppression and warfare in this region means that there are strong family ties and a high premium on demographic expansion at the expense of neighbouring ethnic groups. Group members collectively monitor these high-fertility norms and violations are sanctioned with ostracism. Contraceptive behaviour is forbidden and punishable by temporary exclusion from food-sharing networks.
>
> (2) Fertility is high in this non-industrialized “natural fertility” context (there is little evidence of contraceptive use or parity-specific stopping behaviour). People rely on traditional life-ways and a dense kin-network to support cooperative breeding. Women that use contraception have fewer resources and occupy marginal social network positions, which may indicate lower phenotypic quality or strategic birth spacing to avoid maternal depletion, to optimize reproductive output.

These statements could both be true. But they offer very different insights into the causal structure of fertility behaviour. It is important to qualify the causal claims of the second vignette with those of the first and vice versa. Doing so reveals that what looks like natural fertility may in fact be a highly deliberate and strategic use of reproduction for socio-political aims (see also Kanaaneh 2002). Take, for example, a point of apparent convergence between evolutionary and anthropological demographers: the — at first glance counter-intuitive — use of “modern” contraceptives to increase rather than decrease fertility in parts of sub-Saharan Africa (Bledsoe and others 1998, 1994; Johnson-Hanks 2002; Mace and Colleran 2009; Borgerhoff Mulder 2009; Alvergne and others 2013). The two sub-fields interpret the same behaviour similarly, but under different theoretical assumptions. Anthropological demographers have interpreted this behaviour as consciously strategic: women use modern contraceptives to optimally space births *in order* to achieve high fertility within a particular cultural context (Bledsoe and others 1994; Caldwell and Caldwell 1987). Evolutionary demographers, in contrast, typically focus on the inferences they can make about underlying trade-offs, for example, how improving mortality rates lead to increased competition between children, generating incentives to space births or slow down reproduction (Alvergne and others 2013).

High Fertility Is Neither a State of Nature, Nor Culturally Determined

The foregoing discussion raises broader issues related to how high fertility levels are characterized beyond anthropology and demography. First, contemporary high fertility is often thought to be culturally determined, exemplified in much public and even academic discourse about reproduction in the international development literature. In contrast, the low fertility of women in WEIRD (Henrich and others 2010) societies is often characterized as highly autonomous and somehow outside the realm of cultural norms. The example in Germany shows that this is not the case. Why should it be the case anywhere? We should instead assume that in all populations, reproduction is both negotiated by individuals and enculturated in them by the context they live in, subject to conscious and unconscious biases, and part of the feedback cycle between demographic, ecological and cultural conditions. This will help us avoid problematic distinctions between culturally constrained versus autonomous decision-making, as well as the problematic classification of some groups as in a state of natural fertility and therefore “traditional”, frequently on the basis that they have many children, and others as “controlled” or “modern” because they have very few.

A second issue relates to how ancestral high fertility in human societies is often conceptualized. Here culture is rarely invoked, and fertility rates are seen as largely ecologically determined. Influential models related to the Neolithic transition, some of which take human behavioural ecology as their explanatory framework (Kennett and Winterhalder 2006), have regularly characterized reproduction in largely energetic terms. This same tendency is also reflected in more recent modelling on the ecological sustainability of the human population (e.g. Weinberger and others 2017). In general, there is a revealing disjunct between how transitions to high fertility are theorized compared to transitions to low fertility. In the words of the palaeo-demographer Bocquet-Appel:

> The major difference between the two demographic transitions is that the cause of the NDT [*Neolithic Demographic Transition*] was unconscious, determined by the mechanical effect on maternal energetics of the invention of the agricultural economy, while the essential cause of the CDT [*Contemporary Demographic Transition*] was conscious, the will to control mortality and reproduction. (Bocquet-Appel 2009).

Naturalizing high fertility as the logical physiological outcome of resource availability is problematic for many reasons, chief among which is that it downgrades the causal power of culture in creating high fertility contexts. If we agree that both low and high fertility in contemporary contexts are plausibly driven by cultural evolutionary dynamics, shouldn’t we apply the same principles to ancestral fertility? While we know that fertility rates among extant, and presumably, ancestral hunter-gatherers are low compared to those of farmers (Bentley and others 1994, 1993), this difference is most often interpreted in terms of resource constraints on reproduction, much less in terms of cultural ones. Recent cultural evolution work has begun highlighting how the cultural features of “small-scale”, egalitarian socio-political systems can influence demographic patterns. For example, social norms that level the reproductive playing field in a population via suppression of the reproduction of high status individuals, may be an important strategy for maximizing both within and between-group cooperation (Gavrilets and Fortunato 2014; Bowles 2006). This is a kind of *reverse-dominance*, where the weak can combine forces to dominate the strong, and such mechanisms are thought to be a fundamental feature of hunter gatherer social organization (Boehm 2001), which has important implications for our understanding of their demography.

The transition to farming was as much about changing cultural processes, inter-group dynamics and the rise of new kinds of inequality as it was about the nutritional or ecological benefits of changing resource-availability. And we know that in Europe at least, the process of population growth during the Neolithic was not smooth. Boom-and-bust population dynamics (Shennan and others 2013) strongly indicate endogenous causes of population fluctuations, rather than climatic events. The first farmers were not as successful in their cultivation of crops as were hunter gatherers in their own subsistence activities (Bowles 2011) and the transition came with steep increases in a range of diseases and pathologies, increasing mortality rates (Bocquet-Appel 2011). The general picture is of higher fertility as an adaptive response to higher morbidity and mortality (Page and others 2016) in which cultural processes tend to play, if anything, a minor role. But simulation-work has shown that it would have taken a joint emergence of cultural institutions and technological innovations to explain why new, initially less profitable and higher-risk subsistence practices would have been consistently adopted and maintained by ancestral hunter gatherers (Bowles and Choi 2013). Cultural mechanisms including rules regulating appropriate behaviour, property rights, marriage and dispersal would all have contributed to reproductive ideologies. Complex exchange and trade networks were also a key feature of the Neolithic transition (Ibáñez and others 2015) and these networks would have contributed significantly to the diffusion of new cultural information and technologies, as well as buffering the risk of losing this accumulated culture (Derex and Boyd 2016; Powell and others 2009). How culturally mediated reproductive decisions contributed to these dynamics is as yet unknown. A better understanding of the mechanistic basis of reproduction and how it scales up to generate population-level patterns has enormous contributions to make to our interpretation of these changes in our evolutionary history.

Expanding the Toolkit for Studying Reproduction

Hammel (1990) outlined three components of an anthropologically respectable theory of culture for demography: (1) micro-level explanatory mechanisms grounded in demographically-relevant social networks; (2) appreciation that social information is continuously updated, modified and anticipated by interlocutors, and (3) a much stronger reliance on indigenous or emic categories and interpretations, via detailed ethnography.

The first of these is already well established in evolutionary anthropology, with social networks becoming a major focus in recent years. Although relatively little of this work has focused on demographic questions, social networks have been embraced as a means to capture the dyadic and interconnected influences on reproductive and contraceptive decision-making (Mace and Colleran 2009; Alvergne and others 2011; Colleran and Mace 2015; Borgerhoff Mulder 2009). This work builds on seminal work by demographers in the 1990s and 2000s (Kohler and others 2001; Rutenberg and Watkins 1997; Bongaarts and Watkins 1996; Montgomery and others 1998; Behrman and others 2002) and is an important route to integrating cultural evolutionary theory into evolutionary demography. For example, demographic work has shown that opinion leaders and people with central social network positions have a disproportionate influence on women's contraceptive use and ideation (Valente and Pumpuang 2007; Gayen and Raeside 2010; Kincaid 2000; Gayen and Raeside 2007), consistent with prestige-bias models of cultural evolution (Richerson and Boyd 2005). The specific contraceptive methods that a community ends up endorsing can be highly path-dependent when women rely on their social networks for contraceptive information (Entwisle and others 1996; Kohler 1997). Threshold effects have been shown to be important, as has the size, composition and density of ego-networks, all of which can enable rapid dissemination of new information that facilitates behavioural and cultural change or by strongly reinforcing anti-contraceptive norms (Montgomery and Casterline 1996; Kohler and others 2001; Colleran and Mace 2015; Colleran 2020). The network structure of larger meta-populations can also change the rate at which cultural change proceeds both within and between communities (Borenstein and others 2006; Derex and Boyd 2016; Powell and others 2009).

Second, the continuous nature of social information updating is less well formalized in evolutionary demography, although the state and context-dependent nature of theorizing in human behavioural ecology can handle stochastic or frequency-dependent change in ecological or cultural circumstances. Work focusing on how exogenous institutional or economic changes, for example changing land inheritance practices, have affected reproductive outcomes allows us to make inferences about changing parental investment decisions (Gibson and Gurmu 2011; Colleran 2014). A greater focus both on this kind of research and on even finer-grained perceptions of and attitudes to social change (Schaffnit and others 2019) will help to understand how the costs and benefits of reproduction are interpreted.

Third, the incorporation of "insider" viewpoints and detailed ethnography is much needed. Some evolutionary researchers engaged in long-term field research include discussion of proximate mechanisms to contextualize the results of their work, but this remains a minority. There is much to be gained through a deeper engagement with the insights as well as the publishing models from anthropological demography. Demographic categories and research protocols that we as WEIRD researchers take for granted are often inaccurate (Hruschka and others 2018). Survey instruments are in some cases overly blunt. We must not give up the idea that participant observation and a deep engagement with ethnographic literature can yield transformative insights for our field, leading to new hypotheses, models or approaches — this is as true for human behavioural ecology as it is for cultural evolution. Evolutionary researchers have largely embraced the challenge of explaining culture using quantitative models, but we should not assume that the theoretical landscape has been fully explored. Theory emerges as much from the iterative feedback that comes from regular close attention to the lived experience of our interlocutors as it does from the theorizing we engage in from a distance.

But evolutionary anthropologists differ significantly from other anthropologists in their publication practices, focusing more on short-form scientific publications, with almost no extended ethnographic work or monographs. Anthropological demographers are notable for their contributions to both genres. While some disciplinary journals such as *Human Nature* welcome descriptive or ethnographic articles, many evolutionary anthropologists struggle to have their work accepted in flagship anthropology journals, in part because of an anti-evolution bias, further discouraging them from investing in ethnographic writing. One way forward may be to develop new venues and approaches for the publication of ethnography with numbers.

Closer attention to ethnography brings many benefits: it may help avoid the polarization between cultural and economic determinants of reproduction (Pollak and Watkins 1993) and de-emphasize the distinction between proximate and ultimate causation that is sometimes inappropriate when talking about contemporary reproductive contexts. Instead, a focus on the multilevel and co-evolutionary nature of human demographic behaviour is needed. This highlights that different parts of the system of demography are driven by different evolutionary processes. Perhaps we can partition the understanding and analysis of fertility behaviour into different conceptual components: for example, the origins, spread and maintenance of low fertility behaviour (Colleran 2016). Each of these can be tackled with different methods and data, but under a common framework that provides tools to connect the different parts.

It is in providing these connections that a broader cultural evolutionary framework is useful. This also makes room for reciprocal causation (Laland and others 2011), emergent properties (Smaldino 2014) and group level causation (Richerson and others 2014), all of which necessitate that macro- and micro-level phenomena are not merely reduced to one another. It should lead us to take the spatial and social structures of human populations more seriously, as well as the interactions between different parts of a population, because they generate both boundaries and conduits to cultural diffusion, changing patterns of (cultural) evolution. The identification and measurement of these patterns will help us to better understand the patterning of reproductive outcomes and to highlight the power-dynamic, structural and institutional contexts of reproduction. Evolutionary demographers have examined socioeconomic patterns in reproductive trade-offs, especially in highly developed economies (Fieder and others 2005; Nettle and Pollet 2008; Barthold and others 2012). However much less research has focused on interactions between different social strata (Colleran and others 2014).

Finally, it is important to recognize that the time frames over which we as empirical researchers work (a few generations at most) may not generalize well to evolutionary time scales. We know, for example, that in the mid to long-term, low fertility does not seem to provide a clear fitness benefit for individuals, though it certainly seems to pay off socioeconomically (Goodman and others 2012). There are trade-offs between the rather "myopic" short-term scales of behavioural adaptation and the longer-term adaptations of groups and lineages. This does not mean we cannot study these dynamics in an evolutionary context, but it does mean that we probably can't easily generalize from the logic of one generation's trade-offs in a particular population to the reaction norms of the evolutionary past (e.g. Baldini 2015). We should not abstract away the historical events that generate meaningful interventions in the cultural life of populations, and which alter the conditions for reproductive decision-making in ways that may have nothing to do with fitness maximization.

Concluding Remarks

This chapter is a first attempt to sketch out what a broader cultural evolutionary approach to evolutionary demography might look like. Demographic behaviour is part of the "complex whole" of behaviour, the webs of significance as Geertz put it, that we have spun and in which we are suspended (Geertz 1973). Reproductively relevant behaviours are learned and acquired as part of the cultural repertoires of social groups that have particular histories and value systems. Of course, these are coevolving with the fundamental ecological and energetic constraints of a place and time. But the implications and benefits of bringing "culture" closer to the core of evolutionary demographic thinking, are enormous. Doing so requires addressing the interrelations between culture and demography through different disciplinary traditions, at different levels of analysis, from different causal directions and through mechanistic thinking that engages with ethnography. Rethinking some of our basic assumptions about human reproduction is part of this endeavour.

No one should pretend that this will be an easy undertaking, or that we yet have all the tools we need. One obvious place to start is by incorporating cultural evolutionary theory, which currently combines population-genetic thinking (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985) with psychological models from social psychology and behavioural economics to model the transmission of culture, as well as macro level analyses of path-dependent cultural change (Mesoudi 2011). Even here we do not yet have a ready-made quantitative landscape laid out before us, waiting to be applied judiciously to demographic behaviour. If the measurement of culture and its impact on population dynamics were straightforward, we would not have the tortuous history of anthropology that we do.

But while theoretical developments continue in modelling and experimental approaches to cultural evolution, we need ethnographic work to develop it further. More than any other evolutionary research field, evolutionary demographers are engaged in the complexities of fieldwork and the very real challenges of trying to quantify human social life. They already grapple with the tensions between qualitative and quantitative research and the difficulties of combining "insider" (emic) and "outsider" (etic) perspectives, either explicitly in their writings or pragmatically in their fieldwork (Mulder and others 1985; Wiessner 2016; Colleran and Mace 2011; Roth 2004). Nonetheless, they can often find themselves in what feels like an epistemological no-man's land, being neither completely committed to abstract models nor completely engaged in the kind of thick description typical of socio-cultural anthropology. This position should be seen as a strength and not a weakness, since these researchers are well placed to bridge the quantitative/interpretive gap as a result. Evolutionary anthropologists should feel free to pursue exploratory research that may not be immediately quantifiable. Some of course do this already, but ethnography has been greatly undervalued and underserviced in comparison to quantitative analysis.

By incorporating culture more fully into evolutionary demography, both in terms familiar from cultural evolutionary research and in terms familiar from socio-cultural anthropology, perhaps the different paradigms can become less mutually invisible. In doing so we would do well to avoid rehashing debates that have already occurred in demography, which are highly relevant to the (cultural) evolutionary analysis of reproductive behaviour. Whether a more interdisciplinary evolutionary demography requires that individual researchers employ varied research methods, or that different disciplinary specialists come together, is difficult to gauge (Bernardi and Hutter 2007). Whatever combination of the terms "evolutionary", "cultural", "anthropology" and "demography" we decide to use, here I join other evolutionary anthropologists committed to making an integrated anthropology a basic component of evolutionary research (Fuentes 2016; Hewlett 2016; Wiessner 2016). A renewed enthusiasm for the insights of our colleagues in socio-cultural anthropology and greater engagement with proximate mechanisms, rather than avoiding them in the service of ultimate arguments, will undoubtedly expand and enrich the theoretical and empirical foundations of evolutionary demography.

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