



Invited Anniversary Essay

# Human behavioral ecology and its evil twin

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Human behavioral evolutionary studies tend to interpret behavioral diversity in terms of either “culture” or ecology. Although human behavioral ecology and cultural evolution seem to be different fields, their protagonists often taking different approaches and generating different conclusions, they are in fact 2 kinds of explanation that are hard to tell apart in the real world. Many studies of the evolution of human behavior situate behavior in the context of ecological, cultural, and social environments. The task now is to test explicit evolutionary models against real-world data, preferably on different scales. Cultural phylogenetics and social network analysis have been employed to help in this task, used within the framework of behavioral ecology.

**Key words:** cultural evolution, cultural phylogenetics, human behavioral ecology, proximate, social networks, ultimate.

I am delighted to contribute an essay to this issue of *Behavioral Ecology* on its 25th anniversary on the topic of Human Behavioral Ecology. I wanted to take the opportunity this essay provides to reflect on how the field has progressed from the personal perspective of someone who has worked in this field. In particular, I want to discuss the relationship between human behavioral ecology and culture. Those working in the human sciences are almost always studying culture, whether their papers use the word or not. I include human behavioral ecologists in that group.

The evil twin (in case you were wondering) is a device used in many different fictional genres (usually TV). The evil twin is the antagonist. Evil twins are physical copies of the protagonists, but with radically inverted moralities. My favorite evil twin story by far is Jessica, the evil twin of Niki, in the TV series *Heroes*. If you missed it, and do not have time to catch up the 77 episodes in which Ali Larter appeared as both characters between 2006 and 2010, then suffice it to say that Niki is a stripper, devoted mother of a genius child; Jessica is her scary, back-from-the-dead twin who has superhuman strength, frequently used to pull people apart. Niki's presence is often inconvenient, to say the least, but she does have a habit of saving her sister. Much of the time the viewer cannot tell who is who. Officionados of *Heroes* would say Jessica is technically not a “real” twin but an *alter ego* of Niki (who is suffering a serious personality disorder). So the metaphor is even better—only when embracing her *alter ego* did Jessica become exceptional with unnaturally powerful attributes.

## A BRIEF RECENT HISTORY OF THE STUDY OF THE EVOLUTIONARY BASIS OF HUMAN BEHAVIOR

Ignoring Darwin and others from the 19th and early 20th century, the first modern use of sociobiology as applied to humans was really in the final chapter of E.O. Wilson's 1976 book of that name (Wilson 1980). The territory of studying human behavior was, of course, already occupied by the social and historical sciences, not to mention the humanities, long before evolutionary behavioral scientists became involved. Anthropology is the most relevant of those disciplines, with its historic focus on explaining cultural diversity. However, many of the social sciences, particularly anthropology, have a history of antagonism toward evolutionary approaches to human behavior. The reasons for this have been much reviewed elsewhere (Seegerstrale 2000; Perry and Mace 2010; Colleran and Mace 2011) and are not the topic of this article. Anthropology has now largely divided into 2 disciplines (social and cultural anthropology on the one hand and evolutionary anthropology on the other). Few social anthropologists are interested in or trained to use scientific methodology, often using approaches from the humanities, so whether or not any of the original reasons for the split are resolved, epistemologies are now so different that it seems unlikely the approaches will converge.

Those interested in the evolutionary side of the human behavioral sciences emerged from a range of different human sciences, of which anthropology was the main one (Chagnon and Irons 1979); researchers from each discipline brought with them their own methodologies. Human behavioral evolutionary studies were soon described as falling roughly into 3 main schools of thought: evolutionary psychology (often experimental studies seeking universal psychological adaptations), gene–culture or cultural evolution (generally focused on theoretical models of cultural evolution), and human behavioral

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ecology (Laland and Brown 2002). The last 2 are primarily interested in explaining variation in human behavior. Although they seem to be different fields, taking different approaches, often generating different conclusions, they are in fact 2 fields that are becoming almost the same and sometimes indistinguishable.

Culture was considered explicitly from an evolutionary perspective in gene–culture coevolution or cultural evolutionary studies in papers as old as sociobiology itself (Feldman and Cavalli-Sforza 1976; Lumsden and Wilson 1980). From an evolutionary perspective, culture has a biological basis and is expressed as socially transmitted information grounded in psychological capacities for symbolic thought, language, and learning (Boyd and Richerson 1985; Durham 1992; Richerson and Boyd 2005; Mesoudi et al. 2006). The ability to learn cultural norms from others can be adaptive in the Darwinian sense if it enables efficient information transmission without the need for trial and error individual relearning; thus, socially inherited behaviors, ideas, beliefs, and values are accumulated over generations (Henrich and McElreath 2003; Mace et al. 2005; Mesoudi 2011).

Behavioral ecologists start from the premise that natural selection works on behavior to maximize fitness. They use 3 main approaches to test adaptive hypotheses about the evolution of behavior: experimentation, testing the predictions of theoretical models, and the comparative method (Krebs and Davies 1993). When a particular adaptive model fails to explain observed phenomena, the usual *modus operandi* is to seek a better model, assuming that some vital cost or benefit has been overlooked; hence, our understanding of the evolutionary basis of that behavior is enhanced by ruling out multiple alternative explanations. One of the criticisms of human behavioral ecology is that it ignores culture. I should add that the reverse criticism that cultural evolutionary studies frequently ignore behavioral ecology also needs to be advanced. However, culture is a problematic word, which is causing semantic difficulties in understanding the evolutionary basis of human social behavior. Most anthropologists gave up trying to define culture sometime ago although the anthropological notion of cultural norms generally involves some concept of sanction for those who do not conform (so variation alone is not enough to denote a norm). Evolutionarily minded anthropologists and biologists tend to define cultural behavior simply as behavior that is socially transmitted. This sounds like a simple concept, but in fact, it is too broad a definition to be very useful; just about everything humans do is likely to involve some element of social learning, which is extremely hard to measure in real-world settings. The old nature–nurture debate taught us that all forms of behavior have components of genetic and environmental influence in its development, and there is little benefit in returning to debates about how much of each is relevant in which behavior; that is a different question from those relating to the evolutionary basis of behavior. Furthermore, we need to add the third option of social transmission, if we do not consider the social environment to be part of the ecological environment. In practical terms, most human behavioral ecologists actually consider culture as either part of the environment that is relevant to the behavior they are trying to predict (such as the nature of the hunter–gatherer band, or a matrilineal or patrilineal kinship and descent system that dictates who disperses), or some aspect of culture is the behavior they are trying to predict (such as the marriage norms associated with a particular subsistence system). Social transmission is considered a proximate level of explanation, not necessarily an essential part of understanding the ultimate selective advantage of the behavior in question (Tinbergen 1963). Ignoring proximate mechanisms when identifying models of optimal behavior is often described as the “phenotypic

gambit.” Mechanisms are not considered as unimportant; behavioral ecologists are said to use this gambit if they just assume that they do not alter the optimal strategy and its ecological correlates.

Evolutionary anthropologists have always taken models from behavioral ecology and cultural evolution—considering both as part of the evolutionary biology of human social behavior (Chagnon and Irons 1979), even if studies tended to be defined as falling into the sphere of one or other of the 2 topics rather than being fully integrated. Many of the perceived differences between cultural evolutionary studies and human behavioral ecology are down to the traditions in which those who studied it were trained and, hence, the instincts of the practitioners. Cultural evolutionary scientists traditionally focused on models of the type used in population genetics but rarely tested them empirically. Behavioral ecologists obviously also use models but have a much stronger empirical tradition of testing evolutionary hypotheses about behavior in experimental or in natural contexts. In anthropology, the experimental manipulation of cultural or environmental conditions is usually not possible in a naturalistic setting. Sometimes it is possible to make use of development interventions or similar to find “natural experiments” (such as Gibson and Mace 2006). Comparative studies examining natural variation are often all that is available. Empirical studies examining variation in human behavior have described the behavioral diversity observed as cultural (almost by definition if it is associated with different ethnolinguistic groups), but often that variation is implicitly or explicitly taken as evidence for some explanation based on cultural transmission—an assumption that usually remains untested (e.g., Henrich and coauthors associate the existence of variation in economic games behavior as evidence for cultural group selection; Henrich et al. 2012). The instinct of the behavioral ecologist is to presume ecological differences underpin that variation, by influencing costs and benefits of behaviors at the individual level (Lamba and Mace 2011, 2012). This latter proposition can be tested to some extent by correlating the relevant behavior with ecological variables, without necessarily invoking any particular model for the proximate mechanism by which that variation arises in individuals or societies. Simple correlates of behavioral variation that identify the importance of particular kinds of cultural transmission are harder to identify. Population size and structure are relevant to the potential for cultural transmission (although population size is usually described as an ecological or demographic variable rather than a cultural one and could also be considered a proxy for ecological differences). Population density is thought to underpin the emergence of complex modern human culture in the first place (Powell et al. 2009). A huge rise in social network analysis has helped to try and identify possible pathways for social transmission. However, even when such data are collected, the evidence is still correlational, making the direction of causality hard to infer, as has long been appreciated by social scientists (Manski 1993). It is a general problem with correlational studies that they often cannot be explicit about the evolutionary processes that generate the associations observed.

## CULTURAL TRANSMISSION AND SOCIAL INHERITANCE AS A SOURCE OF MALADAPTIVE BEHAVIOR

Our capacity for cumulative cultural evolution is the single most important trick that enabled the human species to be so successful. We used our culturally acquired skills to inhabit almost all territories on earth and to outcompete all the other hominins. Therefore, it is ironic that probably as much attention has been focused on

explaining how cultural transmission (or social learning) could generate apparently maladaptive aspects of human behavior than has focused on cultural transmission's benefits in helping humans adapt to their environments. But these evolutionary puzzles have received attention because these are some of the more intriguing questions for evolutionary anthropologists. Alongside our self-evident success as a species, we exhibit some behaviors that do not appear to be good for our genes. Culture may sometimes lead us astray from fitness maximization.

The most obvious explanation for maladaptive behavior is a rapid change of environment. If some aspect of society, or indeed any part of a person's environment, has recently changed in ways that would not have occurred before during human evolutionary history, then the proximate mechanisms for social learning or other determinants of behavior (such as preferences) evolved in environmental conditions that are no longer current, and emergent behavior may no longer promote fitness. Natural selection takes time to work. This is sometimes referred to as "mismatch" or "evolutionary lag." How quickly individuals respond to changing cues is still relatively unexplored. The question of how long behavioral adaptations take to evolve is likely to vary with context. A number of studies have given us a window on the pace of genetic evolution in the face of cultural changes in subsistence practices. Lactose tolerance has evolved multiple times among those keeping livestock for dairy (Bersaglieri et al. 2004; Ingram et al. 2009), alleles protective against prion-based neurodegenerative disease (kuru) in the Fore of New Guinea have been selected for by cannibalism (Mead et al. 2009), and the frequency of alleles associated with alcohol dehydrogenase appear to map the history of rice cultivation in south Asia (Peng et al. 2010). These all provide demonstrations of recent strong selection causing rapid evolution, occurring within the last few thousand years or less, in genetic traits associated with changes in subsistence and diet. The complexities of behavioral genetics and epigenetics mean that clear signatures of how specific genes influence behavior are likely to remain more elusive. Some have argued that cultural evolution may have in fact caused genetic evolution to accelerate (Hawks et al. 2007), perhaps by generating so many new niches. Alternatively, the flexibility of behavior may make changes in genes relating to behavioral adaptation evolve more slowly than those related to digestive adaptation, and/or niche construction by humans could be a mechanism by which we can avoid mismatches between their environment and their optimal living conditions (Odling-Smee et al. 2003).

Because generalized social learning rules may promote the spread of a cultural trait, but not necessarily the inclusive fitness of the person performing the associated behavior(s), some evolutionary anthropologists take the position that cultural inheritance mechanisms can generate stable outcomes that result in behaviors that are not necessarily adaptive in the genetic sense (Boyd and Richerson 1985) but will nonetheless persist. Social learning enables cultural traits to move between individuals in a non-Mendelian way. Many cultural traits are copied directly from biological parents, but it is also true that learning rules might involve a range of possible "cultural parents" chosen on grounds of frequency of contact, proximity, prestige, efficacy, or any other criteria; such processes are sometimes referred to as biased transmission. Variation in the possible modes of cultural transmission can, therefore, influence the types and dynamics of cultural behaviors that evolve. For example, the transmission mode of conformist bias (copying the common cultural traits in your group) can cause cultural groups to resist invasion by mutant cultural types, even if there is gene flow between them. This could allow between-group cultural variation to be maintained long enough to be subject to cultural group

selection; this might lead to the evolution of traits that favor the group (Richerson and Boyd 2005). However, the cultural evolution of traits that spread via their benefits to the whole group might be rather slow (Soltis et al. 1995).

One example of a model of how transmission mechanisms alone can be invoked to explain the widespread occurrence of an apparently maladaptive behavior is presented in Tanaka et al (2009). They explore the role of social learning mechanisms in explaining the persistence of self-prescribed medical treatments that have no efficacy: so-called "traditional," "alternative," and even some modern medical treatments. In this example, individuals are modeled to copy self-medication treatments in proportion to the rate at which they observe those treatments being used by other individuals suffering similar medical conditions to themselves. This very interesting paper makes some counterintuitive predictions, including, for example, that if a user takes the treatment for a longer period of time because the illness does not get better, then the opportunity for her to become a model for other social learners increases (Tanaka et al. 2009). In a similar vein, it has been shown that we are more likely to talk about cases where a treatment happened to work than when it did not, biasing the perception of the public in efficacy of useless treatments, and thus further enhancing their spread (de Barra M, Strimling P, Eriksson K, personal communication). Hence, this behavior might persist because in general social learning is more effective than trial and error but can lead to copying useless or even harmful traits in some circumstances. This is essentially a proximate explanation for why a harmful or neutral behavior might persist. However, one might expect humans to improve their learning mechanism over time; perhaps using a more sophisticated rule about when and when not to use social learning could enhance inclusive fitness in the long run. Thus, the explanation for persistence of the use of ineffective medical treatments becomes based either on constraints (the task at hand is simply beyond the capacity of the human mind to resolve) or a "mismatch" argument at the level of the mechanism, which is set to random copying or a simple copying rule. This is not to say these models do not provide convincing proximate explanations for the observed phenomena of useless self-medication. It should also be noted that there are adaptive hypotheses for selection for decision rules that may allocate more resources to curing ourselves when given a placebo that we believe may be helping us to recover (Trimmer et al. 2013).

There is some debate about whether it is correct to refer to cultural evolutionary models of this kind as simply proximate explanations (Laland et al. 2011), given that cultural traits are socially heritable. Cultural traits and biological traits (insofar as they can be classified as such) do coevolve; culturally constructed environments exert selection pressures on behavior, including the mechanisms that control the behavior (which could lead to genetic change not only in humans, as discussed, but possibly in some other species such as dolphins; Kopps et al. 2014), so the 2 processes are not distinct. Some like to argue that memes have their own ultimate-level explanation regarding how good they are at being transmitted, but I prefer not to use the same vocabulary for that. This could be considered a semantic argument, although semantics in science often carry scientific baggage that can be unhelpful. I see no problem with describing cultural evolutionary models based on social transmission and social inheritance as proximate hypotheses, even if cultural transmission is changing gene frequencies, because this distinction makes clear that both proximate questions (relating to how information is transmitted) and ultimate explanations (that relate to how fitness is enhanced) are not mutually exclusive. But whatever words we use, progress on most of the questions in this

area is not going to be made by worrying about definitions, without more empirical work. Cultural evolutionary models have as yet rarely been parameterized by fitting to data sets from real behavior and are often only supported (if at all) by the observation that the general phenomena described does exist. Even the assumptions on which many causative models are based have not often been tested in any detail. So as yet it is hard to know how frequent cases of truly maladaptive behavior, arising due to social transmission, really are.

Meanwhile, back at the ranch, those primarily interested in animal behavior have been exploring reasons why “irrational” behavior could emerge under natural selection, particularly in complex environments (Fawcett et al. 2014). Having to learn about their environment is a constraint humans and animals share, and learning rules may have evolved to make assumptions that are usually but not always helpful; for example, interpreting trends in good or bad returns as meaningful could be optimal when autocorrelation generally occurs due to a trend in environmental change, but not useful when they could occasionally be just runs of good or bad luck. It is also true that the state of the organism can have counterintuitive influences on optimal behavior. But even without these phenomena, it is sometimes true that natural selection over the long term will favor behavioral strategies that violate rules of economic rationality. For example, the addition of a third option could change the order of preference of the first 2 options in a sequential decision-making scenario, violating the economic logic of transitivity; if a less preferred “fallback” choice is added in some scenarios, it allows a more risky option to become the favorite when it would have been rejected when the “fallback” was not present (McNamara et al. 2014). This work emphasizes, as do many cultural evolutionary models, that it is the behavioral strategy that is under selection, not the observed behavior. It also highlights the danger of blaming “culture” for anything that looks like irrational behavior in humans.

## TESTING HYPOTHESES ABOUT THE ORIGIN OF HUMAN CULTURAL BEHAVIORS

There is no theoretical reason why the study of human cultural adaptation should not be investigated in roughly the same manner as behavioral ecologists seek adaptation in the natural world although human studies can present additional challenges. In anthropology, experimental manipulation of cultural or environmental conditions, such as subsistence system, are rarely possible in a naturalistic setting. Sometimes it is possible to make use of development interventions or similar events to find “natural experiments” (Gibson and Mace 2006). But usually we have to rely on natural variation. Optimality models are very useful and have been used to show how human behavior can be understood as adaptive in certain environments in a number of domains, including foraging strategies and reproductive scheduling. These approaches examine individual-level variation within populations. These individual-level effects can also be used to explain wider cultural differences, although cultural differences are, almost by definition, a property of the group rather than a property of the individual. When interpreting cultural differences then, a cross-cultural comparative method becomes a key tool. Cross-cultural comparison was indeed the historical basis of anthropology.

One example of a study that formally evaluates explicit evolutionary models and that is notable for being a rare cultural or gene–cultural coevolutionary study in which models are fitted to real data is the simulation of Itan et al. (2009) of the spread of agriculture and lactase persistence across Europe. It presents a gene–culture coevolutionary model of the emergence of lactose tolerance

(lactase persistence into adulthood) as an adaptation to milk drinking, in a population where individuals can switch between gathering, farming, and pastoralism. Lactase persistence shows a strong latitudinal gradient in Europe, which on the face of it supports the hypothesis that it is selected for in ecological conditions with low levels of sunshine due to vitamin D deficiency (Flatz and Rothauw 1973). Itan et al. fit some of their model parameters explicitly, by using Bayesian inference (Beaumont et al. 2002) to determine which parameters of the model best predict the present day distribution of the allele associated with lactose tolerance in Europeans (known as *-13910-T*). This exercise in statistical inference not only locates the likely starting point of this gene–cultural coevolutionary process in central Europe about 7500 years ago but also shows that the latitudinal gradient in the *T* allele is not due to stronger selection at high latitudes but simply due to the demographic history of the wave of expansion generated by an increasing density of farmers taking over new territory to the north (Itan et al. 2009). The genes for lactase persistence ride on the crest of the wave of advance of territories occupied by the new subsistence strategies, rather than work their way back into existing populations. Holden and Mace (1997) also found no evidence for the vitamin D hypothesis for lactase persistence using a phylogenetic comparative method. Itan et al. show that a model based on demic expansion best explains the patterns of the allele distribution observed today (which, incidentally, they estimate has not yet reached equilibrium). Hence, both proximate models of emergence and ultimate adaptive function are addressed together in a coevolutionary model of subsistence change and human biology. This study shows both the possible dangers of taking ecological correlates as evidence of adaptation (Mace and Jordan 2011) and of the presumption that there has been enough time for optima to be reached. The “phenotypic gambit” is indeed a gambit in human evolutionary studies.

There have been attempts over the last decade or so to evaluate different evolutionary models for the origin of cultural norms empirically, and here, I give some examples from a couple of areas of interest to cultural evolutionary anthropologists—the evolution of cross-cultural variation in human social organization and the demographic transition to low fertility. In the first case, I show how cultural phylogenetics, that uses the cultural history of populations to track their biocultural evolution, has thrown light on questions of how ecology or other factors shape aspects of our social organization. In the second case, a range of approaches examining variation within populations, including social network analysis, are helping us to understand this apparently “anti-Darwinian” behavior.

## The evolution of cross-cultural variation in human social organization

Hunter–gatherers lived in bands, probably with (serially) monogamous marriage, no heritable wealth of consequence, and relatively egalitarian social systems. Extant hunter–gatherer groups are relatively fluid associations of groups of nuclear families, which can be based on matrilineal or patrilineal kinship or friendship or convenience (Marlowe 2005; Hill et al. 2011; Apicella et al. 2012). But it is hard to know to how well extant groups reflect the past. Most ethnography is confined to the present and recent history, relying on living memory or on written or oral histories as sources. Social systems rarely leave any trace in the archaeological record. Sex-specific genetic patterns are often argued to reflect aspects of past human mating systems (Seielstad et al. 1998; Kayser et al. 2003), although such inferences are hard to situate in time, possibly picking up genetic patterns generated after the advent of agriculture and are influenced

by several other aspects of populations structure (Wilkins and Marlowe 2006; Heyer et al. 2012). After the origins of agriculture, and hence heritable wealth, we think patterns of marriage, residence, descent and inheritance, and political hierarchy became both more formalized and more diverse and with more sex-biased dispersal.

Phylogenetic comparative methods provide a powerful set of statistical tools that have been developed by evolutionary biologists and behavioral ecologists for understanding diversity, and these methods go beyond just seeking correlation to examine a whole host of evolutionary processes and questions, including rates of change, ancestral states, the tempo and mode of evolution, phylogenetic signal, and reticulation (Pagel 1999). Cultural phylogenetic techniques make use of language phylogenies to do similar analyses across human cultures (Mace and Pagel 1994) and potentially enable us to put prehistory back into anthropology. Strong phylogenetic signal can often be found within language families even in cases where there is extensive genetic mixing and hence genetic trees would be hard to construct. This is because languages rarely hybridize and migrants (and their children) usually adopt the language of their new cultural group very quickly. Language phylogenies are particularly useful for understanding the last few thousand years of cultural change. One of the major advantages of modern phylogenetic comparative methods is that they enable us to discern between explicitly defined alternative evolutionary models. These methods have been used to show that in Bantu-speaking populations in Africa, patrilineal social systems were associated with pastoralism, whereas matrilineal systems were associated with a lack of cattle keeping (Holden and Mace 2003). The hypothesis is that when there is a mode of subsistence where resources can be monopolized by males to attract females (in this case, cattle), then polygynous marriage emerges; this makes male-biased wealth inheritance optimal as wealth enhances male reproductive success more than it does for females, and hence, it is a better parental investment strategy to pass cattle on to sons. The phylogenetic comparative methods specifically evaluate different models for the direction of change and the one that best fits the data confirms the hypothesis that a transition to pastoralism preceded switches to patrilineal descent systems, helping to build the case for the mode of subsistence determining the kinship system.

Phylogenetic techniques rely on using the extant distribution of traits and the phylogeny, to infer which evolutionary processes were most likely to have generated that distribution (Pagel 1999; Pagel and Meade 2006). Implicit in those methods is the inference of ancestral conditions. We have used these techniques to show that the most likely ancestral condition of Proto-Malayo-Polynesian (~4500 years ago) was matrilineal and matrilocal, with patrilocal systems evolving later on in the Austronesian family (Jordan et al. 2009). Similarly, we have been able to show that dowry and monogamy were probably ancestral in Indo-Europeans (Fortunato et al. 2006). Although studies of ancestral condition do not necessarily demonstrate adaptation, they are essential in arbitrating between different causal hypotheses for the origins of cultural traits. For example, if the ancestral Indo-Europeans were monogamous, then monogamy long predates the emergence of Christianity (which is only about 2000 years old), contradicting the common assumption that Christianity is the driving force behind European monogamy. It supports the notion that prevailing local social systems and conventions generally determine the origin of religious rules rather than vice versa. By comparing different historical models of the evolution of political complexity in the Austronesian language family, Bayesian phylogenetic methods and model comparison show that complexity appears to emerge as a cumulative process, in the sense of that there is a regular pattern of progression from bands

to chiefdoms to complex chiefdoms to states, but the reverse is not true (Currie et al. 2010); although more complex societies can only emerge from slightly less complex ones, the way back down can be more chaotic, with states occasionally collapsing or giving rise to the simplest, or indeed any other kind, of society. All these studies use data on cultural diversity visible in the present to infer the past and are thus reliant on the quality of data and statistical methods available to them, but they all have the advantage of being explicit about the evolutionary models that are being tested and can thus be challenged and potentially improved on. They all address long-standing anthropological questions that ethnographic, genetic, and archaeological methods alone cannot resolve.

### The puzzle of low fertility

A dramatic and near-universal decline in family size was one of the most pervasive social changes of the last 2 centuries and one that continues apace around the world. The society most of us live in has been described as WEIRD—Western, Educated, Industrialized, Rich, and Democratic (Henrich et al. 2010), and the largely urban, industrial, or postindustrial environment where WEIRD societies are found is very different from that in which our ancestors evolved. The very rapid change in mortality, economy, and nutrition in our recent history has occurred in the blink of an eye on an evolutionary timescale. There is no clear agreement on how to interpret this demographic transition, but it is possible that proximate mechanisms evolved under different circumstances may be leading us toward far from optimal fertility decisions from an evolutionary perspective. Demographers have traditionally placed great emphasis on the reduction in infant mortality as the primary causal factor of fertility decline. There is no doubt it is one driver of the transition to low birth rates, although it is less clear whether or why it is associated with smaller families of surviving children. Its failure to predict all aspects of fertility decline lead some to propose cultural transmission of a new idea as a major determinant (Coale and Watkins 1986). In contrast, evolutionary demographers and anthropologists have always focused on high parental investment as key (Borgerhoff Mulder 1998).

It has long been recognized that maximizing reproductive success is not necessarily about maximizing fertility alone, going right back to the pioneering work of ornithologist David Lack (Lack 1954). A “Darwinian demon” that reproduced at the maximum rate is unlikely to succeed in the real world as there will be costs of reproduction to the mother (and probably also to the father), and there will be competition between the many siblings for parental resources. Trading off these costs with the fitness benefits of fertility is known as a “quantity–quality” trade-off and is ultimately what behavioral ecologists would predict determines the nature of human reproductive decisions. Reproductive rate can coevolve with wealth transfers (usually gifts at marriage or through inheritance), limiting optimal fertility in circumstances when the cost of these transfers is high (Mace 1998). It is possible that parental investment can snowball subject to a “runaway” process driven by competition between individuals favoring “quality” over quantity of offspring (Hill and Reeve 2005; Mace 2008). This could potentially make competition between siblings for parental investment more, not less, in modern societies. However, the reproductive decisions of those of us with small families do not appear to maximize our genetic fitness, despite the numerous social, financial, health-related, educational, and other individual benefits associated with low fertility (Goodman, Koupil, & Lawson 2012).

Cultural evolutionary models have raised the possibility that low fertility could be the result of “prestige-biased copying.” In societies

where social success and reproductive success are no longer positively correlated, perhaps due to modern contraception, a predisposition toward copying successful people could mean copying low fertility (Boyd and Richerson 1985). More generally, cultural evolutionary theorists have argued that models of “cultural group selection” could ensure that either conformity and/or punishment could lead to the maintenance of cultural differences between groups; competition between these groups could then favor any cultural behavior that benefits the group (Richerson and Boyd 2005). Limiting fertility, or any other trait that leads to reproductive leveling in groups (such as food sharing), could be examples of behaviors that evolved in this way. Paths of cultural influence are not as easy to identify as one might imagine. In rural Gambia, we found no evidence that kin were influencing the decision to use modern contraception, either by their presence or by their behavior (Mace and Colleran 2009). In rural Ethiopia, we found little evidence that the decision to start using contraception was spreading by copying friends or family in the immediate proximity or by copying those in your immediate social network, suggesting a limited role for social transmission, although religious affiliation did have an effect (Alvergne et al. 2011). This was also the case in rural Bangladesh (Munshi and Myaux 2006). Meanwhile land inheritance does predict contraceptive uptake in both Ethiopia and Bangladesh, with those with private landholdings to pass on to their children being more likely to use contraception (Gibson and Gurmu 2011; Shenk et al. 2013); this suggests low fertility is coevolving with wealth inheritance as behavioral ecological models predict (Mace 1998). The well-known influence of women’s (and men’s) education on fertility might be considered as much a cultural effect as it is an economic one. When evaluating the relative importance of cultural versus cost/benefit variables in their impact on fertility decline, Shenk et al (2013) had to categorize education (a major driver) as both “cultural transmission” and “costs and investments,” illustrating how a dichotomy between explanations based on culture and cost/benefit is often a somewhat unrealistic prospect in real-world settings. Local cultures impose local costs and benefits (e.g., some religions may punish some behavior more than others). Cultural transmission is one of the ways that humans learn that costs and benefits have changed or perhaps might change in the future; so costs and benefits and cultural transmission are both important and have complementary effects. It has been argued that education itself enhances the cultural transmission of low-fertility norms through populations (Ihara and Feldman 2004; Borenstein et al. 2006). To examine this, a good place to start is to examine the local patterns of variation at multiple levels of population structure. In villages in rural Poland in the midst of demographic transition, women of similar socioeconomic status have lower fertility in a better-educated village than in a less-educated village, providing some support for this view (Colleran et al. 2014). Lower socioeconomic status women in well-educated villages had more well-educated women in their social networks. Getting details of social structure and behavioral variation within and between populations makes the task of the human behavioral ecologist far more data intensive than it may have been in the recent past, as they will now preferably get data on behavioral variation over a large number of connected communities, rather than just one or a few (as has been the usual method of anthropological data collection). But such efforts, if they are possible, will be rewarded by clearer insights into our behavior.

If we settle for the notion that an idea is curbing our fertility to a level that is not maximizing our genetic fitness, then we have to consider the notion that over evolutionary time, high-fertility norms will reestablish themselves. This seems unlikely to me. Whatever its

evolutionary basis, the decision rule that is generating low fertility appears to be both persistent and widespread, soon to be generating low fertility globally.

## CONCLUSIONS

The question for evolutionary anthropologists now is not whether behavior is “determined by culture,” but what is the evolutionary basis of that cultural behavior and of cultural norms. The toolkit familiar to behavioral ecologists is a vital part of the efforts to understand the evolutionary basis of human cultural behavior. The combination of a human proclivity for social transmission and social inheritance, in addition to the rapid changes in our physical and social environment (themselves mostly brought about by our capacity for accumulating culture), potentially make the task more complicated than it might be in some other species. Evolutionary models based on optimal strategies and cultural transmission may be distinguishable on paper (or in silico), either as separate or integrated models, but in the real world we do not usually know what we are dealing with. Human behavioral ecology and cultural evolution are twins that are hard to tell apart. One can rarely afford the luxury of dealing with one without the other. It is safest to assume you are dealing with both.

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