

Modernizing Evolutionary Anthropology

Introduction to the Special Issue

Siobhán M. Mattison¹ · Rebecca Sear²

Published online: 10 September 2016
© Springer Science+Business Media New York 2016

Abstract Evolutionary anthropology has traditionally focused on the study of small-scale, largely self-sufficient societies. The increasing rarity of these societies underscores the importance of such research yet also suggests the need to understand the processes by which such societies are being lost—what we call “modernization”—and the effects of these processes on human behavior and biology. In this article, we discuss recent efforts by evolutionary anthropologists to incorporate modernization into their research and the challenges and rewards that follow. Advantages include that these studies allow for explicit testing of hypotheses that explore how behavior and biology change in conjunction with changes in social, economic, and ecological factors. In addition, modernization often provides a source of “natural experiments” since it may proceed in a piecemeal fashion through a population. Challenges arise, however, in association with reduced variability in fitness proxies such as fertility, and with the increasing use of relatively novel methodologies in evolutionary anthropology, such as the analysis of secondary data. Confronting these challenges will require careful consideration but will lead to an improved understanding of humanity. We conclude that the study of modernization offers the prospect of developing a richer evolutionary anthropology, by encompassing ultimate and proximate explanations for behavior expressed across the full range of human societies.

Keywords Human behavioral ecology · Evolutionary behavioral anthropology · Modernization · Demography · Biomarkers · Mixed methods

It is no wonder that, after more than a century and a half of anthropological inquiry, *diversity* continues to form the foundation of anthropologists’ efforts to understand humanity

✉ Siobhán M. Mattison
siobhan.mattison@gmail.com

¹ Department of Anthropology, University of New Mexico, Albuquerque, NM, USA

² London School of Hygiene and Tropical Medicine, London, UK

(Borgerhoff Mulder and Schacht 2012; Nettle 2009). More than ever before, humans inhabit an incredible diversity of socioecological environments, with variable kinship (Shenk and Mattison 2011) and subsistence (Bowles et al. 2010) systems giving rise to, and in turn being shaped by, increasingly complex sociocultural milieus (Richerson and Boyd 2001). Although the story of human evolution partially accommodates such diversity—with many explanations of humans' rise to dominance predicated on behavioral flexibility (Wells and Stock 2007)—the socioenvironmental diversity inhabited by contemporary humans is unprecedented. The aim of evolutionary anthropology is to provide explanatory accounts of human diversity that make sense in light of our evolutionary history. It has historically adopted the anthropological tradition of focusing on small-scale subsistence societies (e.g., Cronk 1991; Laland and Brown 2011) but is making increasing forays into modern and modernizing populations. It is now time to ask how well evolutionary anthropology's theory and methods accommodate the socioecological complexity of contemporary environments. The purpose of this introduction and of this special issue is to address this question. We argue that, although specific challenges are inherent to this endeavor, evolutionary anthropology—largely because of its synthetic and progressive approach to neo-Darwinian evolutionary processes and outcomes—is up to the task.

The issue that we address here is not novel. Indeed, there has been a long-standing debate between some psychologists (EP for short) and anthropologists (usually now referred to as human behavioral ecologists, or HBE) who use an evolutionary approach to understand human behavior, based in part on divergent *a priori* expectations that contemporary behavior may be (HBE) or is not likely to be (EP) adaptive (e.g., Smith 2000; Stulp et al. 2016a [this issue]). This difference of opinion was also a major component of an earlier debate between sociobiologists and Gouldian biologists (e.g., Gould and Lewontin 1979) that has continued to divide anthropologists focused more strongly on the possible adaptive value of behavior versus privileging other explanations for human biology and behavior, respectively (see also Sear 2016a). Yet we feel there is now an increasingly urgent need to understand the behavior and biology of humans in modernizing and modern settings as well as how modernization affects human populations. We must therefore ask whether the theory and methods of evolutionary anthropology are up to the challenge. In other words, how well does the standard toolkit of evolutionary anthropology, including field-based data collection among small-scale, “traditional” societies, accommodate the study of modernizing societies? How do traditional questions of evolutionary anthropology—questions about human foraging, cooperation, and parental investment—apply to modernizing settings? What new methods and areas of theory might be added to the traditional toolkit to improve understanding of human diversity in modernizing contexts? This endeavor may also be helped by greater integration between those subdisciplines that study human psychology, behavior, and biology, as well as greater integration with the non-evolutionary social and health sciences, which have traditionally focused on understanding the mechanisms that influence human behavioral and biological outcomes rather than on their ultimate, evolutionary function. Studying modern and modernizing populations alongside small-scale populations in evolutionary anthropology should help resolve debates about the extent to which human physiology and behavior are adaptive in different environments and should provide more complete accounts of human

diversity, including mechanistic, developmental, historical as well as evolutionarily functional explanations.

What Is “Modernization” and Why the Urgency?

The terms “modern” and “modernization” have been defined in numerous ways by authors in the social sciences (e.g., Inglehart and Baker 2000; Spencer 2009). We use “modernization” somewhat loosely here (but see below) to encapsulate any of the various processes by which self-sufficient, subsistence-based, small-scale (i.e., “traditional”) societies transition away from low-intensity and relatively localized means of living. This definition allows for a number of processes, including acculturation to neighboring cultures (Veile et al. 2014), industrialization and economic development (cf. “modernization theory” in development economics; see Inglehart and Baker 2000), to kick-start and maintain modernization. When we refer to “modern” societies, we mean those societies that have moved through the demographic and epidemiological transitions and now have low fertility and mortality rates. We recognize that these definitions are both loose and relative. This is intentional. Our focus in this article is on the practice of evolutionary anthropology in modern and modernizing societies, as opposed to the effects of modernization on evolutionary outcomes, *per se*.

By contrast, evolutionary anthropologists who are interested in the study of modernization itself should use a more precise definition to operationalize this process (e.g., Newson and Richerson 2009) and should consider the mechanisms of modernization that are relevant to the specific outcomes (behavioral or biological) under investigation. If modernization encapsulates any of the various processes by which a society moves from a relatively traditional to a more modern state, then (1) these terms (“modern” and “traditional”) should be defined clearly and in context-specific ways and (2) a clear causal model should be implied by their definition. So, for example, Mattison (2010) has shown that economic development accompanied by tourism is associated with departures from matriliney among the Mosuo of southwest China. To express this in terms of “modernization” would require a statement of the “traditional” state (i.e., matriliney) from which a society departs, as well as the processes (here, economic development, increased emphasis on material wealth) driving departures toward novel states.

Modernization as defined above may proceed by various pathways, including processes arguably driven from within a given population (e.g., certain types of industrialization, economic development, rise of formal education) and those driven from outside (e.g., market integration, importation of medical technologies, acculturation to neighboring cultures). Given a historical focus on small-scale populations, modernization as studied by many evolutionary anthropologists often arises in conjunction with market integration (e.g., Henrich et al. 2010),¹ involving exposure to and eventual adoption of the technologies, values, and institutions of “mainstream” society (i.e., the market society seen to be the source of influence for the more “traditional”

¹ Although historical demography is another common approach to this issue (see, e.g., Clarke and Low 2001; Voland 2000).

society; Sam and Berry 2010, cited in Veile et al. 2014). As such, it presents a nexus for investigations of evolutionary dynamics from multiple theoretical perspectives: Cultural evolutionary theory sheds light on the dynamics and mechanisms of social learning such as might arise during acculturation; human behavioral ecology considers how human behaviors change in response to different, including novel, socioecological settings; and many related areas (e.g., reproductive ecology, niche construction theory; see Brown 2016 [this issue]) address the mechanisms linking these new settings to functional outcomes, including health.

Our definitions emphasize the general features of modernization that drive the movement away from traditional living, while allowing for culturally specific differences in pathways and cultural products. It must also be stressed that we do not equate modernization with evolutionary (or other kinds of) unilineal progression or with “advanced” (vs. “primitive”) civilization (see Spencer 2009). The view that contemporary hunter-gatherers have evolved less than other, more modernized populations has no basis in evolutionary anthropology and has been dealt with elsewhere (e.g., Hawkes et al. 1997; Marlowe 2005). Nor do we attach any value (moral or otherwise) to what is sometimes referred to as “modernity” or to its counterpart, commonly labeled “traditionalism” (cf. Spencer 2009). In contrast, we mean strictly to describe a process that has now, in all likelihood, affected all of the world’s populations to some degree such that *no extant society* may be characterized as “untouched” by the processes and products of modernization (Inglehart and Baker 2000).

These definitions are also meant to recognize that “modernization” as it proceeds today will appear different than modernization that continues decades from now, as well as the features of contemporary modernization that would benefit from urgent study. Firstly, modernization as it is happening today is typically accompanied by demographic and epidemiological shifts toward lower mortality (with significant declines in infectious disease mortality) and fertility than has been experienced by our species throughout most of its history (Kirk 1996; Lee 2003; Omran 1971). Taking into consideration that the initial stages of demographic modernization may involve increases in mortality (e.g., due to the introduction of novel infectious disease or nutritional stress) or fertility (e.g., due to improvements in health or changes in cultural practices, such as breastfeeding; Dyson and Murphy 1985; Gibson and Mace 2006; Kramer and Greaves 2007), contemporary modernization may offer an important window into the precise dynamics of, and necessary preconditions for, demographic transitions (Kaplan et al. 2015; Shenk et al. 2013; Snopkowski and Kaplan 2014). Secondly, although human cultural innovations have rapidly expanded over the past 100,000 years, the pace of innovation has increased dramatically since the Industrial Revolution. If this pace continues unabated, the window for capturing certain emerging effects of modernization in subsistence populations is likely narrow. Indeed, although it is clear that modernization has affected and will continue to affect the human species throughout its history in various ways, the changes in subsistence brought by contemporary modernization may provide insights with respect to analogous shifts (e.g., resource intensification, increased sedentism, increased emphasis on material wealth) that were fundamental to recent human evolution (Ullah et al. 2015) and were accompanied by significant changes in health (Larsen 2006; Omran 1971) and inequality (Mattison et al. 2016b; Smith et al. 2010). At the same time, the relative rapidity with which modernization proceeds offers an opportunity to depict the dynamics of certain

large-scale evolutionary processes that would normally operate over millennia.² For example, evidence suggests that social inequality has often arisen relatively gradually from egalitarian origins beginning in the Holocene (Mattison et al. 2016b); depicting how and why egalitarianism erodes under conditions of economic development would shed light on how these processes unfolded during periods for which we have no direct observations. Although this comparison may be limited in various ways (e.g., decision-making under conditions of rapid change is likely to be different from that made under gradually changing conditions; see Nolin and Ziker 2016 [this issue]), the insights gleaned could nonetheless prove significant in adjudicating among various models of behavior change over time.

Despite the rapid expansion of modernization with globalization, relatively few studies have deployed methods or theory from evolutionary anthropology to understand its effects. To the present, the foci of this often sparse literature have been correspondingly somewhat limited. The greatest effort has been made to understand declines in fertility associated with modernization (Borgerhoff Mulder 1998; Sear et al. 2016). Given that modernization typically involves an increase in access to resources, the decline in fertility regularly seen to accompany such changes seems counterintuitive in evolutionary perspective (Vining 1986). Several evolutionary anthropologists have tackled this puzzle, often citing changes in the costs and benefits of rearing children (e.g., Kaplan 1996; Sear and Coall 2011; Turke 1989), which shift trade-offs in the quality and quantity of children resulting from differential parental investment in response to different perceived environmental risks and opportunities (e.g., Gibson and Lawson 2011; Kaplan 1996; Lawson and Mace 2009; Shenk 2009; Shenk et al. 2013). Other approaches include a consideration of how changing cultural norms may contribute to this process (e.g., Boyd and Richerson 1985; Newson et al. 2005; see also Collieran 2016; Kaplan 1996), and some approaches attempt to compare these cost-benefit and cultural models (e.g., Shenk et al. 2013; Snopkowski and Kaplan 2014). Other systematic efforts to understand the effects of modernization include those centered on the evolution of fairness and cooperation (e.g., Henrich et al. 2010), and on changing parenting and reproductive behavior (e.g., Alvergne et al. 2011; Kaplan 1996; Veile et al. 2014), such as Mhairi Gibson's long-term study in Ethiopia exploring how changes associated with modernization have affected reproductive strategies, including the timing of births (Gibson and Mace 2006), reproductive success (Gibson and Gurmú 2011), and parental investment (Gibson and Lawson 2011; Gibson and Sear 2010). Even though our review of the literature has undoubtedly overlooked certain articles that deal systematically with modernization, there is a dearth of such studies, and topics of core interest to evolutionary anthropologists—subsistence, social stratification, altruism, and parental investment, to name a few—are vastly understudied with respect to the effects of modernization.

Most significantly, failing to take into account the influences of modernization can lead to fallacious understandings of important phenomena. For example, Lawson et al. (2015) conducted a study of family structure and child health among 56 ethnically diverse Tanzanian villages at varying levels of modernization. Pooling data across villages, they found that polygynous marriage predicted low food security and poor child health, a pattern that has previously led both evolutionary and population health

² This is not to suggest that human evolution always proceeds slowly.

scholars to conclude that polygynous marriage is a “harmful cultural practice” (Omariba and Boyle 2007). However, when contrasting monogamous and polygynous households to their local neighbors *within* each village, polygynous households were wealthier and their children often exhibited indicators of better health. This implies that, at least in this setting, the association between polygynous marriage and poor welfare may be an artifact of village-level characteristics rather than being due to polygyny, per se. Specifically, Lawson et al. (2015) note that because polygyny is most common in relatively marginalized Maasai villages, it is likely that village-level characteristics, such as poor service provisioning and low rainfall, *cause* poor welfare, whereas polygyny is *associated* with poor welfare because it is more common in marginalized communities. There are undoubtedly many more examples of this type, in which contrasts between “traditional” and modern cultural practices are subject to the “ecological fallacy” (Pollet et al. 2014). Explicit incorporation of population-level indicators of modernization thus has the potential to improve basic science as well as public policy.

Why Does Modernization Present Challenges for Empirical Evolutionary Anthropology?

Because evolutionary anthropology focuses on the mechanisms and outcomes of human evolution and because human environments have changed dramatically over at least the past 12,000 years, until relatively recently, evolutionary anthropologists have tended to prefer studies of small-scale societies (e.g., Laland and Brown 2011; Marlowe 2005; Smith 2000). Although the considerable variation across small-scale societies is recognized, such societies are assumed to have characteristics shared by most populations throughout most of human history, such as high fertility and mortality, low population density, largely self-sufficient (i.e., “autarkic”) subsistence strategies, and relatively limited social stratification (Irons 1998). This historical focus has arguably led to a bias in studies toward relatively smaller or more marginal communities such that more modernized societies have been overlooked by budding anthropologists, partly under guidance to pursue fieldwork in a way that maintains the anthropological status quo, but also perhaps because of the implicit assumption that it is much harder to study humans from an evolutionary perspective in environments where much of their behavior no longer appears to be fitness maximizing. Realistically, this pattern cannot continue. Traditional field sites (i.e., field sites involving societies that are considered relatively remote and autarkic) are increasingly saturated by researchers. Even the most remote contemporary societies have experienced and will continue to experience the effects of modernization. It would be most unfortunate if existing biases led researchers to ignore or distort such effects in presentations of their field settings. The Masai example given above shows that ignoring modernization could lead to important misunderstandings of evolutionarily relevant phenomena. It is, in any respect, clear that we must confront the challenges that modernization presents to our discipline.

Although we are optimistic that evolutionary anthropologists will find ways to surmount associated challenges, it is important not to trivialize their nature or extent. In addition to what we perceive as a disciplinary bias within evolutionary anthropology

that favors the study of less-modernized societies, the study of modernizing societies presents challenges that strike at many of the core tenets of evolutionary anthropological research. In particular, modernizing societies' environments, both cultural and ecological, have some characteristics that are far removed from those experienced by the majority of humans throughout history (Marlowe 2005). This is not entirely problematic for evolutionary anthropology—we have long recognized the importance of behavioral flexibility to human evolution (Borgerhoff Mulder 2004; Wells and Stock 2007; Winterhalder and Smith 2000)—but some of the changes associated with modernization are quite novel and may limit adaptive decision-making or induce “misfiring” of psychological or physiological adaptations. In addition, social and economic networks are increasingly large, and increased urbanization, rising population densities, and technological innovations affect the scale and scope of person-to-person interactions (Newson and Richerson 2009). These factors also affect the speed of perceived socioecological shifts and (adaptive) responses thereto (Nolin and Ziker 2016). A key overarching issue affecting studies of modernized contexts is thus increased complexity: on the one hand, we interact with an increasing proportion of non-kin and individuals with whom we have single-shot interactions; on the other hand, stratification means that meaningful inter-sub-population interactions may be relatively limited. These changes must be carefully considered in studies of modernizing populations.

Additional changes that affect the plausibility and testability of evolutionary hypotheses in modernized contexts include a release of nutritional constraints altering energy balance and changing life history strategies (Wells 2006). Advances in healthcare and sanitation have dramatically altered the demographic profile in modernized settings, reducing mortality, increasing the range of options available to control fertility, and changing the costs and benefits associated with migration, all of which have profound effects on individual life histories. Such demographic and epidemiological changes have also likely marked a shift from selection pressures acting strongly through variation in mortality toward greater selection pressures on reproductive outcomes (Stearns et al. 2010). Increased emphasis on formal education has dramatically changed the costs and benefits of childrearing since it reduces the productivity of children and thereby increases the costs of raising them; this significantly affects the means by which modernized populations achieve reproductive success (Kaplan 1996). This, in conjunction with increased exposure to media, may be driving increasing disjuncture of cultural and reproductive success. Approaches that blend cultural evolutionary and human behavioral ecological theory and methods may be needed to understand resulting shifts in evolutionary dynamics (e.g., Colleran 2016).

All of this together suggests the importance of questioning assumptions about fitness maximization in modernizing societies. Behavioral ecologists in particular have been apt to operate on the premise that many traits maximize fitness, but this heuristic, although useful as a starting place, must be recognized and tested in all domains of evolutionary anthropology. As we advocate below, this can be fruitfully addressed by closer inspections of the mechanisms—psychological, cultural, physiological—that bring behavior about, and it also may benefit from increasingly moving away from more narrow tests of “ultimate” hypotheses about behavior to the exclusion of other insights into evolutionary processes.

Why Study Modern and Modernizing Populations?

There are many reasons to promote the study of evolutionary anthropology within modern and modernizing contexts. Most obviously, there is no way to understand the extent to which the above challenges undermine applications of evolutionary theory to behavior and biology without testing hypotheses in modern and modernizing settings (see Stulp et al. 2016a). But modern and modernizing contexts also provide unique opportunities for testing evolutionary hypotheses. The study of modernizing societies at multiple points in time allows for the opportunity to test predictions about how changes in ecology, including subsistence strategy, may result in changes in behavior (Brown 2016; Kushnick et al. 2016; Nolin and Ziker 2016; and Snopkowski 2016 in this issue all provide examples of this). In particular, “natural experiments” may arise as a result of modernization, if modernization occurs piecemeal across a population. These allow us to study the effects of changes in key variables of interest (e.g., social and economic factors) on behavioral and biological outcomes (Garruto et al. 1999). For example, Mhairi Gibson’s work in Ethiopia used the natural experiments of a development initiative, implemented in some villages but not others, and changes to land tenure policies, to explore how reproductive and parenting behavior changed as a result of modernization (Gibson and Mace 2006; Gibson and Sear 2010; Gibson and Gurmu 2011). In another example, Gurven and colleagues have shown that market integration among the Tsimané of Bolivia, where the level of market integration varied across villages, has led to increased wealth redistribution (Gurven et al. 2015), possibly in association with leaders trying to leverage increased social influence to enhance their status (von Rueden 2014). In this case, the effects of modernization on sharing behavior may provide clues about the more general evolutionary mechanisms by which inequality is thought to arise (Mattison et al. 2016b), which would be difficult or impossible to glean from studies carried out within traditional societies not undergoing the process of market transition.

A further advantage is the widespread availability of secondary data on large-scale populations, both modernizing and modern (Stulp et al. 2016a). With some notable exceptions (Clarke and Low 2001; Low 1991; Volland 2000), evolutionary anthropologists have tended to test hypotheses following the collection of primary data designed for specific purposes. Increasingly, however, evolutionary anthropologists have made use of existing datasets collected within contemporary populations (Nettle et al. 2013), and although such work involves distinct challenges, it also improves on certain inevitable deficiencies of primary data (Stulp et al. 2016a). Such datasets typically have the advantages of large sample sizes, rich data (including demographic, economic, social, health, and occasionally even genetic information), and, often, longitudinal designs. Conducting and interpreting the analysis of data collected by individuals outside of one’s research team is not always straightforward, but Stulp and colleagues [parts I and II, this issue] argue convincingly that such challenges can be thought of as a magnification of the problems faced by researchers analyzing their own data and that researchers can reap specific rewards not otherwise possible, especially in providing insights into the results of aggregated behaviors at the level of larger groups.

Indeed, evolutionary anthropology of large, modern and modernizing populations has led to unique insights about our own culture that are occasionally inconsistent with other social science approaches. That humans engage in risky behavior in the face of unpredictable environments (Hill 1993), for example, offers the possibility that changes

in health behavior may be more quickly achieved by altering the environment than simply by “educating” people to be healthy (Pepper and Nettle 2014; Wells 2014). If sex-biased inheritance patterns are more strongly influenced by the base of subsistence than by cultural diffusion (Mattison et al. 2016a), then altering perceptions about the usefulness of daughters versus sons will require improving social and material opportunities for women. Understanding the differences in the consequences of polygyny, and other supposedly harmful cultural practices, in developing versus more developed contexts may have important implications for policies aimed at influencing such practices (e.g., Gibson and Lawson 2015; Lawson et al. 2015). More generally, an evolutionary framework may often be better equipped to reveal motivations for behaviors that appear suboptimal from other perspectives (e.g., Belsky et al. 1991). For example, some reproductive behaviors, such as “early” childbearing in high-income, low-fertility contexts, may be seen as problematic from the perspective of health because they are assumed to be the cause of “risky” behaviors and negative outcomes in later life (McLanahan 2004). Evolutionary research suggests that these behaviors are likely responses to living in a relatively harsh environment and may be evolutionarily advantageous in contexts where delayed childbearing would lead to lower reproductive success (Nettle 2010; Sheppard et al. 2014).

Finally, including modernizing and modern societies within the framework of evolutionary anthropology strengthens the ability of evolutionary anthropologists to conduct comparative work, which, while increasingly common in evolutionary anthropology (Borgerhoff Mulder et al. 2009; Henrich et al. 2005), has typically focused on small-scale, subsistence societies. Given the importance of comparative work in allowing us to test hypotheses about how different socioecologies may influence behavior, and in making generalizations about our species, it would undoubtedly benefit us to include modern and modernizing societies therein. Doing so would clarify the extent to which there are limits to general rules for human behavior and would also provide evidence of heterogeneity within so-called WEIRD (Western, Educated, Industrialized, Rich, Developed) populations (Stulp et al. 2016a).

The Way Forward Is Not To Throw Back

The study of modern and modernizing populations offers specific challenges and opportunities and must be carefully implemented. As alluded to above, several promising outlets of critical inquiry include (1) the use of secondary datasets that allow for the evaluation of subtle differences in fitness-relevant outcomes (e.g., age at first birth, interbirth interval, parity progression), (2) quantitative (and ideally longitudinal) ethnography of modernizing populations, and (3) cross-cultural and comparative work that allows for systematic investigation of the effects of ecological variation on behavior and fitness (see also Shenk and Mattison 2011). All of this suggests that there is room to extend studies of small-scale hunting-and-gathering populations into the modern age without relying on throwback arguments that insist that contemporary populations have retained behaviors or environments that have been present since the distant past or more generally on arguments that presuppose adaptations are contingent on continuity between an evolutionarily relevant past and the present (Zuk 2013; see also Stulp et al. 2016a).

Tools that will help in this endeavor include novel statistical and computational methods that can deal with complex and hierarchical data to test across multiple levels of explanation (e.g., cultural vs. evolutionary ecological) in comparative framework, and that incorporate the nested effects of individuals within larger populations (e.g., Alvergne et al. 2011; Colleran et al. 2015). To that end, researchers will need to be trained specifically in the use of complex datasets (e.g., in relational database management) and sophisticated analytical techniques. Advanced quantitative methods are not always considered a key part of the training of anthropologists, despite the efforts of some evolutionary anthropologists (e.g., McElreath 2016) to develop and teach sophisticated techniques. The use of large secondary datasets comes with challenges over and above those of analyzing primary datasets, and they require different theoretical and methodological tools: for example, in order to design appropriate analyses for hypothesis-testing given large numbers of potential variables that could be included, and understanding the limited use of p values in contexts where many findings will be significant, but essentially meaningless (see Stulp et al.'s two articles in this issue for further discussion). Model-selection approaches (Towner and Luttbeg 2007) are increasingly used to overcome some of these difficulties (e.g., Borgerhoff Mulder and Beheim 2011; Mattison et al. 2015; Shenk et al. 2013), although in our experience they are often misunderstood by reviewers, such that increased training in their use may be warranted. Theory that explicitly incorporates the links between biological and cultural fitness (e.g., Boyd and Richerson 1985; Feldman and Laland 1996) will also prove useful, especially as empirical tests of these theories remain relatively limited, as do explicit tests incorporating contrasting predictions (cf. Laland et al. 2014). The tools mentioned in this paragraph are useful for, and may have been developed in, the analysis of more “traditional” cultures, but they are essential when considering the particular challenges that working with modernizing and modern populations presents.

To address the challenge that modern populations are not fitness maximizing, we will do well to enhance our efforts to measure fitness-relevant outcomes that are more subtle than fertility, *per se*. Evolutionary anthropology has always incorporated the study of a range of fitness-relevant outcomes, but lifetime reproductive success has typically been used as the “gold standard” measure of fitness. However, measures such as fertility that are commonly used to evaluate the fitness associated with certain behaviors may be of limited use when population norms restrict their variability (e.g., if there is a strong preference for two children; see Stulp et al. 2016b). Rather, it may be worth recognizing that even small differences in the timing of reproduction (e.g., age at first birth), the pace of reproduction (e.g., interbirth interval), or survivorship can produce meaningful differences in fitness over time (Jones and Bird 2014). More proximate measures of physiology may also provide clues as to how current behaviors affect reproductive function. The relationship between hormones, marriage, and parenting has suggested that men’s reproductive physiology responds more strongly to changes in family structure in cultures where fathers routinely invest in childcare, for example (Gettler 2014). This insight is uniquely anticipated by a reproductive ecological framework and underscores the promise of using markers of endocrine and reproductive function in evolutionary ecological work (e.g., Ellison 1994).

The foregoing all suggests that novel methods building on established frameworks will allow for improved understanding of contemporary human behavior and biology and that extensions into the modern are not only inevitable, but also warranted.

Integration across frameworks will facilitate progress by surmounting divisions that sometimes act as impediments to empirical advances. In addition to those referenced in Stulp et al. (2016a), we would advocate repairing apparent divisions between fields seen to stem from sociobiology (typically researchers focused on behavior including those identifying as human behavioral ecologists, as well as evolutionary psychologists) and those favoring a “Gouldian” approach (often labeling themselves as “human biologists”) that sometimes dismisses evolutionary behavioral approaches in humans as storytelling by unscrupulous scientists (cf. Lyle and Smith 2012). Indeed, if success is based in part on applying our findings to inform human welfare, it may be found in research that explores the intersection of the biological, behavioral, and demographic (e.g., Gettler 2014; Gibson and Lawson 2015; Sear 2016b). Rather than viewing behavior as an outcome of often-unspecified cultural processes and biology as shaped by natural selection and other evolutionary processes, a truly integrated *biocultural* approach recognizes the significance of all of these domains and the feedbacks they have with each other (Laland and Brown 2011; Nettle et al. 2013).

The papers in this special issue serve to illustrate both the challenges of, and improved understandings likely to result from, using an evolutionary framework to understand the causes and consequences of modernization. Soler (2016) uses social network analysis and economic games to evaluate how religious leadership maintains social cohesion in contemporary urban Brazil. Snopkowski (2016) provides an in-depth look at the predictors of marital dissolution and remarriage in San Borja, Bolivia, providing an ethnographically informed interpretation of how divorce and remarriage benefit women and their children in a modernizing setting where economic opportunities are now very different for women than they were just decades ago. Nolin and Ziker (2016) distinguish between the effects on fertility of sustained risk and uncertainty that men encounter in Siberia, with an analysis that is highly relevant to understanding broader patterns of modernization and its effects on fitness-relevant behavior. Stulp et al. (2016b) provide an overview of the benefits and challenges of using secondary datasets in modern populations, focusing on the analysis of fertility, as well as an illustrative example of the relationship between wealth and fertility using the NLSY79 database from the United States. Schacht et al. (2016) provide another example of how the analysis of secondary data can suggest alternative interpretations for widespread phenomena—here, using population-level data from the United States to test the hypothesis that an increase in the ratio of adult men to adult women may result in decreased violence among men, rather than increased rates as is commonly postulated. Brown (2016) argues that the incorporation of new theory (niche construction theory) can inform our understanding of behavioral change, specifically in relation to footbinding in China. Kushnick et al. (2016) use vignettes to explore changes in the incidence of and feelings toward consanguineous *impal* marriages among the Karo Batak of Indonesia. Finally, Dunham (2016) tackles an issue of significance to evolutionary anthropologists working in applied areas as she reviews the potential contradictions between modern childbirth (in the US) and possibly evolved predispositions for minimal intervention. Taken together, these articles reinforce that evolutionary arguments are relevant in modern and modernizing settings, with effects on many domains of behavior and biology—from hunting to childbirth—that have formed the traditional foci of evolutionary anthropology.

Conclusion

The effects of modernization are broad and profound and, from a societal perspective, can be viewed as both positive and negative. An evolutionary perspective helps to define the trade-offs inherent to modernization, explaining why intended improvements are sometimes attended by undesired consequences, as well as how the effects of modernization vary in different social, cultural, and economic milieus. In addition to a basic need to depict the effects of modernization as they arise, we have argued that modernization may also provide a unique window into more general processes that have been central to human evolution since the Holocene. As isolated societies are increasingly under threat of disruption or extinction (Walker et al. 2016), anthropologists will need to accept and embrace the opportunities that modernization brings to understanding the evolution of human behavior and biology. Such portrayals will serve to broaden the impact of our findings and, ideally, will feed back positively to the populations that participate in our research, including those many of us inhabit.

Acknowledgments David Lawson and Mary Shenk provided many important insights on this paper that helped to sharpen the discussion. Conversations with the participants of the AAA symposium in which these ideas were developed, including the authors of articles herein and those who were not able to contribute, also stimulated us to think critically about how modernization can be incorporated into evolutionary anthropology. Finally, we thank Charles Darwin for extending insights based on a modern, contrived process [artificial selection] to an invisible, but deeply influential process [natural selection] shaping humanity, past and present.

References

- Alvergne, A., Gibson, M. A., Gurmu, E., & Mace, R. (2011). Social transmission and the spread of modern contraception in rural Ethiopia. *PLoS One*, *6*(7), e22515.
- Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: an evolutionary theory of socialization. *Child Development*, *62*, 647–670.
- Borgerhoff Mulder, M. (1998). The Demographic Transition: are we any closer to an evolutionary explanation? *Trends in Ecology & Evolution*, *13*, 266–270.
- Borgerhoff Mulder, M. (2004). Human behavioural ecology. In *Encyclopedia of life sciences*. Wiley Online. doi:10.1038/npg.els.0003671.
- Borgerhoff Mulder, M., & Beheim, B. A. (2011). Understanding the nature of wealth and its effects on human fitness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 344–356.
- Borgerhoff Mulder, M., Samuel, B., Hertz, T., et al. (2009). Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science*, *326*, 682–688.
- Borgerhoff Mulder, M., & Schacht, R. (2012). Human behavioural ecology. In *Encyclopedia of life sciences*. Wiley Online. doi:10.1002/9780470015902.a0003671.pub2.
- Bowles, S., Smith, E. A., & Mulder, M. B. (2010). The emergence and persistence of inequality in premodern societies. *Current Anthropology*, *51*, 7–17.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Brown, M. J. (2016). Footbinding, industrialization, and evolutionary explanation: an empirical illustration of niche construction and social inheritance. *Human Nature*, *27*(4). doi:10.1007/s12110-016-9268-5.
- Clarke, A. L., & Low, B. S. (2001). Testing evolutionary hypotheses with demographic data. *Population and Development Review*, *27*, 633–660.
- Colleran, H. (2016). The cultural evolution of fertility decline. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1692), 20150152.

- Colleran, H., Jasienska, G., Nenko, I., Galbarczyk, A., & Mace, R. (2015). Fertility decline and the changing dynamics of wealth, status and inequality. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1806), 20150287.
- Cronk, L. (1991). Human behavioral ecology. *Annual Review of Anthropology*, 20, 25–53.
- Dunham, B. (2016). Homebirth midwifery in the United States: evolutionary origins and modern challenges. *Human Nature*, 27(4). doi:10.1007/s12110-016-9266-7.
- Dyson, T., & Murphy, M. (1985). The onset of fertility transition. *Population and Development Review*, 11(3), 399–440.
- Ellison, P. T. (1994). Advances in human reproductive ecology. *Annual Review of Anthropology*, 23, 255–275.
- Feldman, M. W., & Laland, K. N. (1996). Gene-culture coevolutionary theory. *Trends in Ecology and Evolution*, 11, 453–457.
- Garruto, R. M., Little, M. A., James, G. D., & Brown, D. E. (1999). Natural experimental models: the global search for biomedical paradigms among traditional, modernizing, and modern populations. *Proceedings of the National Academy of Sciences*, 96(18), 10536–10543.
- Gettler, L. T. (2014). Applying socioendocrinology to evolutionary models: fatherhood and physiology. *Evolutionary Anthropology*, 23(4), 146–160.
- Gibson, M. A., & Gurmu, E. (2011). Land inheritance establishes sibling competition for marriage and reproduction in rural Ethiopia. *Proceedings of the National Academy of Sciences*, 108(6), 2200–2204.
- Gibson, M. A., & Lawson, D. W. (2011). “Modernization” increases parental investment and sibling resource competition: evidence from a rural development initiative in Ethiopia. *Evolution and Human Behavior*, 32, 97–105.
- Gibson, M. A., & Lawson, D. W. (2015). Applying evolutionary anthropology. *Evolutionary Anthropology*, 24(1), 3–14.
- Gibson, M. A., & Mace, R. (2006). An energy-saving development initiative increases birth rate and childhood malnutrition in rural Ethiopia. *PLOS Med*, 3(4), e87.
- Gibson, M. A., & Sear, R. (2010). Does wealth increase parental investment biases in child education? Evidence from two African populations on the cusp of the fertility transition. *Current Anthropology*, 51(5), 693–701.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London B: Biological Sciences*, 205(1161), 581–598.
- Gurven, M., Jaeggi, A. V., von Rueden, C., Hooper, P. L., & Kaplan, H. (2015). Does market integration buffer risk, erode traditional sharing practices and increase inequality? A test among Bolivian forager-farmers. *Human Ecology*, 43(4), 515–530.
- Hawkes, K., O’Connell, J. F., & Rogers, L. (1997). The behavioral ecology of modern hunter-gatherers, and human evolution. *Trends in Ecology & Evolution*, 12(1), 29–32.
- Henrich, J., Boyd, R., Bowles, S., et al. (2005). Economic man in cross-cultural perspective: behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, 28(6), 795–815.
- Henrich, J., Ensminger, J., McElreath, R., et al. (2010). Markets, religion, community size, and the evolution of fairness and punishment. *Science*, 327(5972), 1480–1484.
- Hill, K. (1993). Life history theory and evolutionary anthropology. *Evolutionary Anthropology*, 2, 78–88.
- Inglehart, R., & Baker, W. E. (2000). Modernization, cultural change, and the persistence of traditional values. *American Sociological Review*, 65(1), 19–51.
- Irons, W. (1998). Adaptively relevant environments versus the environment of evolutionary adaptedness. *Evolutionary Anthropology*, 6, 194–204.
- Jones, J. H., & Bird, R. B. (2014). The marginal valuation of fertility. *Evolution and Human Behavior*, 35(1), 65–71.
- Kaplan, H. (1996). A theory of fertility and parental investment in traditional and modern human societies. *American Journal of Physical Anthropology*, 39, 91–135.
- Kaplan, H. S., Hooper, P. L., Stieglitz, J., & Gurven, M. (2015). The causal relationship between fertility and infant mortality: prospective analyses of a population in transition. In P. Kreaeger, B. Winney, S. J. Uljaszek, & C. Capelli (Eds.), *Population in the human sciences: Concepts, models, evidence* (pp. 361–376). Oxford: Oxford University Press.
- Kirk, D. (1996). Demographic transition theory. *Population Studies*, 50, 361–387.
- Kramer, K. L., & Greaves, R. D. (2007). Changing patterns of infant mortality and maternal fertility among Pumé foragers and horticulturalists. *American Anthropologist*, 109(4), 713–726.
- Kushnick, G., Fessler, D. M. T., & Zuska, F. (2016). Disgust, gender, and social change: testing alternative explanations for the decline of cousin marriage in Karo society. *Human Nature*, 27(4). doi:10.1007/s12110-016-9263-x.

- Laland, K. N., & Brown, G. R. (2011). *Sense and nonsense: evolutionary perspectives on human behaviour*. Oxford: Oxford University Press.
- Laland, K., Uller, T., Feldman, M., et al. (2014). Does evolutionary theory need a rethink? *Nature*, *514*(7521), 161–164.
- Larsen, Clark Spencer (2006) The agricultural revolution as environmental catastrophe: implications for health and lifestyle in the Holocene. In S.A.G. Leroy, H. Jousse and M. Cremaschi (Eds.), *Impact of rapid environmental changes on humans and ecosystems* (pp. 12–20), *Quaternary International* 150(1).
- Lawson, D. W., & Mace, R. (2009). Trade-offs in modern parenting: a longitudinal study of sibling competition for parental care. *Evolution and Human Behavior*, *30*, 170–183.
- Lawson, D. W., James, S., Ngadaya, E., et al. (2015). No evidence that polygynous marriage is a harmful cultural practice in northern Tanzania. *Proceedings of the National Academy of Sciences*, *112*(45), 13827–13832.
- Lee, R. (2003). The Demographic Transition: three centuries of fundamental change. *The Journal of Economic Perspectives*, *17*(4), 167–190.
- Low, B. S. (1991). Reproductive life in nineteenth century Sweden: an evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, *12*(6), 411–448.
- Lyle, H., & Smith, E. (2012). How conservative are evolutionary anthropologists? *Human Nature*, *23*, 306–322.
- Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology*, *14*(2), 54–67.
- Mattison, S. M. (2010). Economic impacts of tourism and erosion of the visiting system among the Mosuo of Lugu Lake. *The Asia Pacific Journal of Anthropology*, *11*, 159–176.
- Mattison, S. M., Wander, K., & Hinde, K. (2015). Breastfeeding over two years is associated with longer birth intervals, but not measures of growth or health, among children in Kilimanjaro, TZ. *American Journal of Human Biology*, *27*(6), 807–815.
- Mattison, Siobhán M., Bret A. Beheim, Bridget Chak, and Peter M. Bustin (2016a) Offspring sex preferences among patrilineal and matrilineal Mosuo in southwest China revealed by differences in parity progression. *Royal Society Open Science*, in press.
- Mattison, S. M., Smith, E. A., Shenk, M. K., & Cochrane, E. E. (2016b). The evolution of inequality. *Evolutionary Anthropology*, *25*(4), 184–199.
- McElreath, R. (2016). *Statistical rethinking: A Bayesian course with examples in R and Stan*. Boca Raton: CRC Press.
- McLanahan, S. (2004). Diverging destinies: how children are faring under the second Demographic Transition. *Demography*, *41*(4), 607–627.
- Nettle, D. (2009). Ecological influences on human behavioural diversity: a review of recent findings. *Trends in Ecology & Evolution*, *24*(11), 618–624.
- Nettle, D. (2010). Dying young and living fast: variation in life history across English neighborhoods. *Behavioral Ecology*, *21*(2), 387–395.
- Nettle, D., Gibson, M. A., Lawson, D. W., & Sear, R. (2013). Human behavioral ecology: current research and future prospects. *Behavioral Ecology*, *24*(5), 1031–1040.
- Newson, L., & Richerson, P. J. (2009). Why do people become modern? A Darwinian explanation. *Population and Development Review*, *35*, 117–158.
- Newson, L., Postmes, T., Lea, S. E. G., & Webley, P. (2005). Why are modern families small? Toward an evolutionary and cultural explanation for the Demographic Transition. *Personality and Social Psychology Review*, *9*, 360–375.
- Nolin, David A., and John P. Ziker (2016) Reproductive responses to economic uncertainty: fertility decline in post-Soviet Ust'-Avam, Siberia. *Human Nature*, *27*(4). doi:10.1007/s12110-016-9267-6.
- Omariba, D. W. R., & Boyle, M. H. (2007). Family structure and child mortality in Sub-Saharan Africa: Cross-National effects of polygyny. *Journal of Marriage and Family*, *69*(2), 528–543.
- Oman, A. R. (1971). The epidemiologic transition: a theory of the epidemiology of population change. *The Milbank Memorial Fund Quarterly*, *49*, 509–538.
- Pepper, G. V., & Nettle, D. (2014). Socioeconomic disparities in health behaviour: an evolutionary perspective. In M. A. Gibson & D. W. Lawson (Eds.), *Applied evolutionary anthropology* (pp. 225–243). New York: Springer.
- Pollet, T. V., Tybur, J. M., Frankenhuys, W. E., & Rickard, I. J. (2014). What can cross-cultural correlations teach us about human nature? *Human Nature*, *25*(3), 410–429.
- Richerson, Peter J., and Robert Boyd (2001) Institutional evolution in the Holocene: the rise of complex societies. *Proceedings of the British Academy*, *110*, 197–234.
- Sam, D. L., & Berry, J. W. (2010). Acculturation: when individuals and groups of different cultural backgrounds meet. *Perspectives on Psychological Science*, *5*(4), 472–481.

- Schacht, R., Tharp, D., & Smith, K. R. (2016) Marriage markets and male mating effort: violence and crime are elevated where men are rare. *Human Nature*, 27(4). doi:10.1007/s12110-016-9271-x.
- Sear, Rebecca (2016a) Evolutionary demography: a Darwinian renaissance in demography. In James D. Wright (ed.) *International encyclopedia of the social and behavioral sciences*. Elsevier. https://www.academia.edu/10348377/Evolutionary_Demography_A_Darwinian_renaissance_in_demography, accessed January 28, 2015.
- Sear, R. (2016b). Beyond the nuclear family: an evolutionary perspective on parenting. *Current Opinion in Psychology*, 7, 98–103.
- Sear, R., & Coall, D. (2011). How much does family matter? Cooperative breeding and the Demographic Transition. *Population and Development Review*, 37, 81–112.
- Sear, R., Lawson, D. W., Kaplan, H., & Shenk, M. K. (2016). Understanding variation in human fertility: what can we learn from evolutionary demography? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1692), 20150144.
- Shenk, M. K. (2009). Testing three evolutionary models of the Demographic Transition: patterns of fertility and age at marriage in urban South India. *American Journal of Human Biology*, 21, 501–511.
- Shenk, M. K., & Mattison, S. M. (2011). The rebirth of kinship: evolutionary and quantitative approaches in the revitalization of a dying field. *Human Nature*, 22, 1–15.
- Shenk, M. K., Towner, M. C., Kress, H. C., & Alam, N. (2013). A model comparison approach shows stronger support for economic models of fertility decline. *Proceedings of the National Academy of Sciences*, 110, 8045–8050.
- Sheppard, P., Garcia, J. R., & Sear, R. (2014). A not-so-grim tale: how childhood family structure influences reproductive and risk-taking outcomes in a historical U.S. population. *PLoS One*, 9(3), e89539.
- Smith, E. A. (2000). Three styles in the evolutionary study of human behavior. In C. Lee, N. Chagnon, & W. Irons (Eds.), *Human behavior and adaptation: An anthropological perspective* (pp. 27–46). Hawthorne: Aldine de Gruyter.
- Smith, E. A., Mulder, M. B., Bowles, S., et al. (2010). Production systems, inheritance, and inequality in premodern societies: conclusions. *Current Anthropology*, 51, 85–94.
- Snopkowski, K. (2016) Marital dissolution and child educational outcomes in San Borja, Bolivia. *Human Nature*, 27(4). doi:10.1007/s12110-016-9265-8.
- Snopkowski, K., & Kaplan, H. (2014). A synthetic biosocial model of fertility transition: testing the relative contribution of embodied capital theory, changing cultural norms, and women's labor force participation. *American Journal of Physical Anthropology*, 154(3), 322–333.
- Soler, M. (2016). The faith of sacrifice: leadership trade-offs in an Afro-Brazilian religion. *Human Nature*, 27(4). doi:10.1007/s12110-016-9264-9.
- Spencer, J. (2009). Modernism, modernity and modernization. In *Routledge encyclopedia of social and cultural anthropology*. London: Routledge.
- Stearns, S. C., Byars, S. G., Govindaraju, D. R., & Ewbank, D. (2010). Measuring selection in contemporary human populations. *Nature Reviews Genetics*, 11(9), 611–622.
- Stulp, Gert, Rebecca Sear, and Louise Barrett (2016a) The reproductive ecology of industrial societies, Part I: why measuring fertility matters. *Human Nature*, 27(4). doi:10.1007/s12110-016-9269-4.
- Stulp, G., Rebecca Sear, Susan B. Schaffnit, Melinda C. Mills & Louise Barrett (2016b) The reproductive ecology of industrial societies, Part II: the association between wealth and fertility. *Human Nature*, 27(4). doi:10.1007/s12110-016-9272-9.
- Towner, M. C., & Luttbeg, B. (2007). Alternative statistical approaches to the use of data as evidence for hypotheses in human behavioral ecology. *Evolutionary Anthropology*, 16, 107–118.
- Turke, P. W. (1989). Evolution and the demand for children. *Population and Development Review*, 15(1), 61–90.
- Ullah, I. I. T., Kuijt, I., & Freeman, J. (2015). Toward a theory of punctuated subsistence change. *Proceedings of the National Academy of Sciences*, 112(31), 9579–9584.
- Veile, A., Martin, M., McAllister, L., & Gurven, M. (2014). Modernization is associated with intensive breastfeeding patterns in the Bolivian Amazon. *Social Science & Medicine*, 100, 148–158.
- Vining, D. R. (1986). Social versus reproductive success: the central theoretical problem of human sociobiology. *Behavioral and Brain Sciences*, 9(01), 167–187.
- Voland, E. (2000). Contributions of family reconstitution studies to evolutionary reproductive ecology. *Evolutionary Anthropology*, 9(3), 134–146.
- von Rueden, C. (2014). The roots and fruits of social status in small-scale human societies. In J. T. Cheng, J. L. Tracy, & C. Anderson (Eds.), *The psychology of social status* (pp. 179–200). New York: Springer.
- Walker, R. S., Kesler, D. C., & Hill, K. R. (2016). Are isolated indigenous populations headed toward extinction? *PLoS One*, 11(3), e0150987.

- Wells, J. C. K. (2006). The evolution of human fatness and susceptibility to obesity: an ethological approach. *Biological Reviews*, *81*(2), 183–205.
- Wells, J. C. K. (2014). Nutrition in a changing world: how economic growth drives chronic diseases. In M. A. Gibson & D. W. Lawson (Eds.), *Applied evolutionary anthropology* (pp. 245–270). New York: Springer.
- Wells, J. C. K., & Stock, J. T. (2007). The biology of the colonizing ape. *American Journal of Physical Anthropology*, *134*(S45), 191–222.
- Winterhalder, B., & Smith, E. A. (2000). Analyzing adaptive strategies: human behavioral ecology at twenty-five. *Evolutionary Anthropology*, *9*, 51–72.
- Zuk, M. (2013). *Paleofantasy: What evolution really tells us about sex, diet, and how we live*. New York and London: WW Norton.

Siobhán M. Mattison is an evolutionary ecologist and assistant professor at the University of New Mexico. Her interests focus on human social and demographic behavior, and she studies these in contemporary small-scale, modernizing societies in China and Vanuatu, among other locations.

Rebecca Sear is an evolutionary demographer and human behavioral ecologist at the London School of Hygiene and Tropical Medicine. Her research is interdisciplinary, combining evolutionary biology, anthropology, and demography.