Title: Modernizing evolutionary anthropology

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Keywords: human behavioral ecology, evolutionary behavioral anthropology, modernization, demography, biomarkers, mixed methods

Word count: ~6000, including references

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. Additionally, modernization often provides a source of 'natural experiments', as 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.

Introduction: It is no wonder that, after over a century and a half of anthropological inquiry, *diversity* continues to form the foundation of anthropologists' efforts to understand humanity (Borgerhoff Mulder and Schacht 2001; Nettle 2009). More than ever before, humans inhabit an incredible diversity of socio-ecological environments, with variable kinship (Shenk and Mattison 2011) and subsistence (Bowles, Smith, and Borgerhoff Mulder 2010) systems giving rise to, and in turn being shaped by, increasingly complex sociocultural milieux (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 socio-environmental diversity inhabited by contemporary humans is unprecedented. The aim of evolutionary anthropology is to provide explanatory accounts of human behavioral 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, so that it is now time to ask how well evolutionary anthropology's theory and methods accommodate the socio-ecological complexity of contemporary environments. The purpose of this introduction and of this special issue is to address this question. We argue that, while specific challenges are inherent to this endeavor, evolutionary anthropology – largely due to 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 longstanding debate between some psychologists (EP for short) and anthropologists (usually now referred to as human behavioral ecologists, or HBEers) 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, Sear, and Barrett 2016, 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 (see also Sear 2016a) focused more strongly on the possible adaptive value of behavior versus privileging other explanations for human biology and behavior, respectively. Yet we feel that there is now an increasingly urgent need to understand the behaviors 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 sub-disciplines which 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

47 behavior are adaptive in different environments and provide more complete accounts of
48 human diversity, including mechanistic, developmental, historical as well as evolutionarily
49 functional explanations.
50
51 *What is 'modernization' and why the urgency?*
52 The terms 'modern' and 'modernization' have been defined in numerous ways by
53 authors in the social sciences (e.g., Inglehart and Baker 2000; Spencer 2009). We use the
54 term 'modernization' somewhat loosely here (but see below) to encapsulate any of the
55 various processes by which self-sufficient, subsistence-based, small-scale (i.e.,
56 "traditional") societies transition away from low intensity and relatively localized means of
57 living. This definition allows for a number of processes, including acculturation to
58 neighboring cultures (Veile et al. 2014), industrialization and economic development (cf.
59 "modernization theory" in development economics) (see Inglehart and Baker 2000) to kick
60 start and maintain modernization. When we refer to 'modern' societies, we mean those
61 societies that have moved through the demographic and epidemiological transitions and
62 now have low fertility and mortality rates. We recognize that these definitions are both
63 loose and relative. This is intentional. Our focus in this article is on the practice of
64 evolutionary anthropology in modern and modernizing societies, as opposed to the effects
65 of modernization on evolutionary outcomes, per se.
66 By contrast, evolutionary anthropologists who are interested in the study of
67 modernization itself should use a more precise definition to operationalize this process
68 (e.g., Newson and Richerson 2009), and should consider the mechanisms of modernization
69 that are relevant to the specific outcomes (behavioral or biological) under investigation. If

70 'modernization' encapsulates any of the various processes by which a society moves from a
71 relatively 'traditional' to a more 'modern' state, then: 1) these terms (modern and
72 traditional) should be defined clearly and in context-specific ways as they are employed in
73 studies; and 2) a clear causal model should be implied by their definition. So, for example,
74 Mattison (2010) has shown that economic development accompanied by tourism is
75 associated with departures from matriliny among the Mosuo of Southwest China. To
76 express this in terms of 'modernization' would require a statement of the 'traditional' state
77 (i.e., matriliny) from which a society departs, as well as the processes (here, economic
78 development, increased emphasis on material wealth) driving departures toward novel
79 states.

80 Modernization as defined above may proceed by various pathways, including processes
81 arguably driven from within a given population (e.g., certain types of industrialization,
82 economic development, rise of formal education), and those driven from outside (e.g.,
83 market integration, importation of medical technologies, acculturation to neighboring
84 cultures). Given a historical focus on small-scale populations, modernization as studied by
85 many evolutionary anthropologists often arises in conjunction with market integration (e.g.,
86 Henrich et al. 2010)[1], involving exposure to and eventual adoption of the technologies,
87 values, and institutions of 'mainstream' society (i.e., the market society seen to be the
88 source of influence for the more 'traditional' society) (Sam & Berry, 2010, cited in Veile et al.
89 2014). As such, it presents a nexus for investigations of evolutionary dynamics from
90 multiple theoretical perspectives: Cultural evolutionary theory sheds light on the dynamics
91 and mechanisms of social learning such as might arise during acculturation; human

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

92 behavioral ecology considers how human behaviors change in response to different,
93 including novel, socio-ecological settings; and many related areas (e.g., reproductive
94 ecology, niche construction theory – see Brown, this issue) address the mechanisms linking
95 these new settings to functional outcomes, including health.
96 Our definitions emphasize the general features of modernization that drive the
97 movement away from traditional living, while allowing for culturally specific differences in
98 pathways and cultural products. It must also be stressed that we do not equate
99 modernization with evolutionary (or other kinds of) unilineal progression or with
100 'advanced' (versus 'primitive') civilization (see Spencer 2009). The view that contemporary
101 hunter-gatherers have evolved less than other, more modernized populations, has no basis
102 in evolutionary anthropology and has been dealt with elsewhere (e.g., Hawkes, O'Connell,
103 and Rogers 1997; Marlowe 2005). Nor do we attach any value (moral or otherwise) to what
104 is sometimes referred to as 'modernity' or to its counterpart, commonly labeled
105 'traditionalism' (cf. Spencer 2009). In contrast, we mean strictly to describe a process that
106 has now, in all likelihood, affected all of the world's populations to some degree such that
107 *no extant society* may be characterized as 'untouched' by the processes and products of
108 modernization (Inglehart and Baker 2000).
109 These definitions are also meant to recognize that 'modernization' as it proceeds today
110 will appear different than modernization that continues decades from now as well as the
111 features of contemporary modernization that would benefit from urgent study. Firstly,
112 modernization as it is happening today is typically accompanied by demographic and
113 epidemiological shifts toward lower mortality (with significant declines in infectious
114 disease mortality) and fertility than has been experienced by our species throughout most

115 of its history (Kirk 1996; Lee 2003; Omran 1971). Taking into consideration that the initial
116 stages of demographic modernization may involve increases in mortality (e.g., due to the
117 introduction of novel infectious disease or nutritional stress) or fertility (e.g., due to
118 improvements in health or changes in cultural practices, such as breastfeeding) (Kramer
119 and Greaves 2007; Dyson and Murphy 1985; Gibson and Mace 2006), contemporary
120 modernization may offer an important window into the precise dynamics of and necessary
121 preconditions for demographic transitions (Shenk et al. 2013; Snopkowski and Kaplan
122 2014; Kaplan et al. 2015). Secondly, although there has been a rapid expansion of human
123 cultural innovations over the last 100,000 years, the pace of innovation has increased
124 dramatically since the industrial revolution. If this pace continues unabated, the window
125 for capturing certain emerging effects of modernization in subsistence populations is likely
126 narrow. Indeed, although it is clear that modernization has affected and will continue to
127 affect the human species throughout its history in various ways, the changes in subsistence
128 brought by contemporary modernization reflect subsistence changes that were
129 fundamental to recent human evolution (Ullah, Kuijt, and Freeman 2015) and accompanied
130 by significant changes in health (Larsen 2006; Omran 1971) and inequality (Mattison et al.
131 n.d.; Smith et al. 2010). At the same time, the relative rapidity with which modernization
132 proceeds offers an opportunity to depict the dynamics of certain large-scale evolutionary
133 processes[2] that would normally operate over millennia. For example, evidence suggests
134 that social inequality has often arisen relatively gradually from egalitarian origins
135 beginning in the Holocene (Mattison et al. n.d.); depicting how and why egalitarianism
136 erodes under conditions of economic development would shed light on how these

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

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 are likely to be different from those made under gradually changing conditions; see Nolin and Ziker, 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 largest 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; Turke 1989; Sear and Coall 2011), which shift tradeoffs 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; Lawson and Mace 2009; Shenk 2009; Shenk et al. 2013; Kaplan 1996). Other approaches include a consideration of how changing cultural norms may contribute to this process (e.g., Newson et al. 2005; Boyd and Richerson 1985; see also Kaplan 1996; Colleran 2016); and some approaches attempt to test these cost-benefit and cultural models against one another (e.g., Snopkowski and Kaplan 2014; Shenk et al. 2013). Other systematic efforts to understand the effects of modernization include those centered on the evolution of fairness and cooperation (e.g.,

160 Henrich et al. 2010), and on changing parenting and reproductive behavior (e.g., Alvergne
161 et al. 2011; Kaplan 1996; Veile et al. 2014), such as Mhairi Gibson's long-term study in
162 Ethiopia exploring how changes associated with modernization have affected reproductive
163 strategies , including the timing of births (Gibson and Mace 2006), reproductive success
164 (Gibson and Gurmu 2011), and parental investment (Gibson and Lawson 2011; Gibson and
165 Sear 2010). Even recognizing that our review of the literature has overlooked certain
166 articles that deal systematically with modernization, there is a dearth of such studies and
167 topics of core interest to evolutionary anthropologists – subsistence, social stratification,
168 altruism, and parental investment, to name a few – are vastly understudied with respect to
169 the effects of modernization.
170 Most significantly, failing to take into account the influences of modernization can
171 lead to fallacious understandings of important phenomena. For example, Lawson et al.
172 (2015) conducted a study of family structure and child health among 56 ethnically diverse
173 Tanzanian villages at varying levels of modernization. Pooling data *across* villages, they
174 found that polygynous marriage predicted low food security and poor child health, a
175 pattern that has previously led both evolutionary and population health scholars to
176 conclude that polygynous marriage is a 'harmful cultural practice' (Omariba and Boyle
177 2007). However, when contrasting monogamous and polygynous households to their local
178 neighbors *within* each village, polygynous households were wealthier and their children
179 often possessed indicators of better health. This implies that, at least in this setting, the
180 association between polygynous marriage and poor welfare may be an artifact of village-
181 level characteristics rather than due to polygyny, per se. Specifically, Lawson et al. (2015)
182 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, where 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 last 12,000 years, until relatively recently, evolutionary anthropologists have tended to prefer studies of small-scale societies (e.g., Marlowe 2005; Smith 2000; Laland and Brown 2011). While recognizing that there is considerable variation across small-scale societies, 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 Lawson example 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 which 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 (Winterhalder and Smith 2000; Borgerhoff Mulder 2004; Wells and Stock 2007) - 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. Additionally, social and economic networks are increasingly large, 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 socio-ecological shifts and (adaptive) responses thereto (Nolin et al., this issue). 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 towards 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, while useful as a starting place, must be recognized and tested in all domains of evolutionary anthropology. As we advocate below, this may be fruitfully addressed by closer inspections of the mechanisms – psychological, cultural, physiological – which bring behavior about, and may benefit from increasing movement 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 part I, this issue). 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 (Nolin & Ziker; Brown, Kushnick et al., and Snopkowski 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 such 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. n.d.), 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., part I, this issue). With some notable exceptions (Voland 2000; Clarke and Low 2001; Low 1991), 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 for contemporary populations (Nettle et al. 2013) and, while such work involves distinct challenges, it also improves on certain inevitable deficiencies of primary data (Stulp, Sear, and Barrett 2016). 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. While

298 conducting and interpreting the analysis of data collected by individuals outside of one's
299 research team is not always straightforward, Stulp and colleagues (part I and II, this issue)
300 argue convincingly that such challenges may be thought of as a magnification of the
301 problems faced by researchers analyzing their own data and that researchers can reap
302 specific rewards not otherwise possible, especially in providing insights into the results of
303 aggregated behaviors at the level of larger groups.
304 Indeed, evolutionary anthropology of large, modern and modernizing populations
305 has led to unique insights about our own culture that are occasionally inconsistent with
306 other social science approaches. That humans engage in risky behavior in the face of
307 unpredictable environments (Hill 1993) , for example, offers the possibility that changes in
308 health behavior may be more quickly achieved by altering the environment than simply by
309 'educating' people to be healthy (Wells 2014; Pepper and Nettle 2014). If sex-biased
310 inheritance patterns are more strongly influenced by the base of subsistence than by
311 cultural diffusion (Mattison et al. 2016), then altering perceptions about the usefulness of
312 daughters versus sons will require improving social and material opportunities for women.
313 Understanding the differences in the consequences of polygyny, and other supposedly
314 'harmful cultural practices', in developing versus more developed contexts may have
315 important implications for policies aimed at influencing such practices (e.g., Lawson et al.
316 2015; Gibson and Lawson 2015). More generally, an evolutionary framework may often be
317 better equipped to reveal motivations for behaviors that appear sub-optimal from other
318 perspectives (e.g., Belsky, Steinberg, and Draper 1991). For example, some reproductive
319 behaviors, such as 'early' childbearing in high income, low fertility contexts may be seen as
320 problematic in health perspective, 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 within contexts where delayed childbearing would lead to lower reproductive success (Nettle 2010; Sheppard, Garcia, and Sear 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 (Henrich et al. 2005; Borgerhoff Mulder et al. 2009), has typically focused on small-scale, subsistence societies. Given the importance of comparative work in allowing us to test hypotheses about how different socio-ecologies may influence behaviour, 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, Part I, this issue).

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)

344 ethnography of modernizing populations, and 3) cross-cultural and comparative work that
345 allows for systematic investigation of the effects of ecological variation on behavior and
346 fitness (see also Shenk and Mattison 2011). All of this suggests that there is room to extend
347 studies of small-scale hunting and gathering populations into the modern age without
348 relying on throwback arguments that insist that contemporary populations have retained
349 behaviors or environments that have been present since the distant past or more generally
350 on arguments that presuppose adaptations are contingent on continuity between an
351 evolutionarily relevant past and the present (Zuk 2013; see also Stulp, Sear, and Barrett
352 2016 this issue).
353 Tools that will help in this endeavor include novel statistical and computational
354 methods that can deal with complex and hierarchical data, including comparative data, to
355 test across multiple levels of explanation, including the nested effects of individuals within
356 larger populations and alternative predictions, such as those of cultural evolutionary
357 versus evolutionary ecological hypotheses (e.g., Colleran et al. 2015; Alvergne et al. 2011).
358 To that end, researchers will need to be trained specifically in the use of complex datasets
359 (e.g., in relational database management) and sophisticated analytical techniques –
360 advanced quantitative methods are not always considered a key part of the training of
361 anthropologists, despite the efforts of some evolutionary anthropologists to both develop
362 and teach very sophisticated techniques, such as McElreath's work on Bayesian modelling
363 (e.g., McElreath 2016). The use of large secondary datasets comes with challenges over and
364 above those of analyzing primary datasets, which will require theoretical, as well as
365 methodological, sophistication: for example, in order to design appropriate analyses for
366 hypothesis-testing given large numbers of potential variables which could be included; and

to understand the limited use of p-values in contexts where many findings will be significant, but essentially meaningless (see Stulp et al Parts I and II, this issue for further discussion). Model-selection approaches (Towner and Luttbeg 2007) are increasingly used to overcome some of these difficulties (e.g., Shenk et al. 2013; Mattison, Wander, and Hinde 2015; Borgerhoff Mulder and Beheim 2011), although often misunderstood by reviewers in our experience, 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 present.

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 reproductive success has typically been used as the 'gold standard' measure of fitness. But 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. Part II, this issue). 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

390 in fitness over time (Jones and Bird 2014). More proximate measures of physiology may
391 also provide clues as to how current behaviors affect reproductive function. The
392 relationship between hormones, marriage, and parenting has suggested that men's
393 reproductive physiology responds more strongly to changes in family structure in cultures
394 where fathers routinely invest in childcare, for example (Gettler 2014). This insight is
395 uniquely anticipated by a reproductive ecological framework and underscores the promise
396 of using markers of endocrine and reproductive function in evolutionary ecological work
397 (e.g., Ellison 1994).
398 The foregoing all suggests that novel methods building on established frameworks will
399 allow for improved understanding of contemporary human behavior and biology and that
400 extensions into the modern are not only inevitable, but also warranted. Integration across
401 frameworks will facilitate progress by surmounting divisions that sometimes act as
402 impediments to empirical advances. In addition to those referenced in Stulp et al. (Part I,
403 this issue), we would advocate repairing apparent divisions between fields seen to stem
404 from 'sociobiology' (typically researchers focused on behavior including those identifying
405 as 'human behavioral ecologists', and 'evolutionary psychologists') and those favoring a
406 "Gouldian" approach (often labeling themselves as 'human biologists') that sometimes
407 dismisses evolutionary behavioral approaches in humans as storytelling by unscrupulous
408 scientists (cf. Lyle and Smith 2012). Indeed, if success is based in part on applying our
409 findings to inform human welfare, it may be found in research that explores the
410 intersection of the biological, behavioral, and demographic (e.g., Gibson and Lawson 2015;
411 Sear 2016b; Gettler 2014). Rather than viewing behavior as an outcome of often
412 unspecified cultural processes and biology as shaped by natural selection and other

413 evolutionary processes, a truly integrated *biocultural* approach recognizes the significance
414 of all of these domains and the feedbacks they have with each other (Laland and Brown
415 2011; Nettle et al. 2013).
416 The papers in this special issue serve to illustrate both the challenges of and improved
417 understandings likely to result from using an evolutionary framework to understand the
418 causes and consequences of modernization that result from an evolutionary framework.
419 Montserrat Soler uses social network analysis and economic games to evaluate how
420 religious leadership maintains social cohesion in contemporary urban Brazil. Snopkowski
421 provides an in-depth look at the predictors of marital dissolution and remarriage in San
422 Borja, Bolivia, providing an ethnographically informed interpretation of how divorce and
423 remarriage benefit women and their children in a modernizing setting where economic
424 opportunities are now very different for women than they were even just decades ago.
425 Nolin and Ziker distinguish between the effects on fertility of sustained risk and
426 uncertainty that men encounter in Siberia, with an analysis that is highly relevant to
427 understanding broader patterns of modernization and its effects on fitness-relevant
428 behavior. Stulp and colleagues provide an overview of the benefits and challenges of using
429 secondary datasets in modern populations, focusing on the analysis of fertility, as well as an
430 illustrative example of the relationship between wealth and fertility using the NHANES
431 database from the US. Schacht and colleagues provide another example of how the analysis
432 of secondary data can suggest alternative interpretations for widespread phenomena –
433 here, using population-level data from the US to test the hypothesis that an increase in the
434 ratio of adult men to adult women may result in decreased violence among men rather than
435 increased rates as is commonly postulated. Melissa Brown 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 and colleagues use vignettes to explore changes in the incidence of and feelings toward consanginueous *impal* marriages among the Karo Batak of Indonesia. Finally, Bria Dunham 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, may be viewed as both positive and negative. An evolutionary perspective helps to define the tradeoffs 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 milieux. 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, Kesler, and Hill 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 feedback positively to the populations that participate in our research, including those many of us inhabit.

Acknowledgements: 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.

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