Human Behavioral Ecology, in "The Princeton Guide to Evolution" Edited by Jonathan B Losos

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VII.11

Human Behavioral Ecology

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OUTLINE

1. Development of human behavioral ecology
2. Problems and criticism
3. New focus on evolution in the modern societies
4. What can human behavioral ecology contribute to the general study of evolution?

Human behavioral ecology applies the general theories and mathematical models developed for understanding variation in traits across species to test similar questions in humans. The focus is on studying the consequences of particular traits or behavioral strategies for an individual's success at passing on its genes to the following generations, given the ecological and social environment of that individual. Humans experience a wide global range of living conditions and lifestyles, from traditional communities to extreme urbanization, and human behavioral ecologists today use a range of study designs and data sources to investigate all these populations from an evolutionary perspective. The type of data available on humans makes it possible to investigate the details of many central questions in evolutionary biology.

GLOSSARY

Cohort Studies. Longitudinal study designs commonly used, for example, in medical and social science research, and increasingly also in human behavioral ecology. Such studies record the life events of a group (cohort) of individuals sharing a common characteristic or experience (e.g., born during the same year or exposed to a famine in utero) and compare these individuals with other cohorts or the general population.

Demographic Transition. The transition from high birth and death rates to low birth and death rates as a country develops from a preindustrial to an industrialized economic system.

(Historical) Population Records. Registers of births, deaths, marriages, and migrations that have been maintained in many countries over long periods of time (e.g., by the church or governmental departments) and that are now a frequent source of data in human behavioral ecology.

Hunter-gatherer. Ancestral subsistence mode of *Homo* in which most or all food was obtained from wild plants and animals, in contrast with agriculture, which relies on domesticated species. All humans were hunter-gatherers at least until approximately 10,000 years ago.

Intervention Studies. Procedures used to test a cause-and-effect relation in epidemiological studies by modifying the suspected causal factor(s) affecting health outcomes (e.g., by supplementary feeding of a group of subjects or treating them with a given medicine) and recording their future life events in comparison with those of subjects not receiving the treatment.

Microevolution. A change in gene frequency within a population over time.

Optimality Models. Simulations that weigh the costs and benefits of a given trait or behavior compared with another trait or behavior for maximizing fitness.

Pleistocene. A time period 2,588,000 to 12,000 years before the present when key events in human evolution took place.

Twin Registers. A type of data often used in human behavioral genetics recording various traits of up to thousands of twin pairs from a given country or cohort. Such data sets are most commonly used to estimate the relative importance of environmental and genetic influences on particular traits and behaviors in humans by comparing individuals in identical and fraternal twin pairs.

Human behavioral ecology is an evolutionary approach to studying human behavior that applies methods virtually identical with those used by behavioral ecologists studying other species. The focus is on studying the consequences of particular traits or behavioral strategies for an individual's success at passing on its genes to the following generations. The most successful behavior from the viewpoint of evolutionary fitness may vary among individuals depending on attributes such as their wealth, age, living environment, family support available, or set of genes. Empirical studies in human behavioral ecology use data from different human populations to test predictions produced by the general theories and mathematical models developed for understanding variation in traits across species. One of the most widely studied questions is whether variation among individuals in partner choice and reproductive patterns in humans is adaptive: Does mate choice capitalize on reproductive prospects in the future? Does age at first reproduction reflect the "best age" for the given man or woman to start a family to maximize his or her overall number of children reared over a lifetime? Or is there an adaptive explanation for women going through menopause before the end of their life span? For example, it is postulated that women living in an environment with a high mortality hazard benefit from giving birth at a young age to ensure reproducing before dying, despite the risks to both maternal and baby survival associated with early motherhood. In contrast, a woman living in a more stable environment might maximize her overall number of surviving offspring by delaying the onset of motherhood until she has finished growing and maturing.

Application of evolutionary theory to understanding human behavior has grown increasingly popular since the publication of *Sociobiology* by Edward O. Wilson (1975), often considered as "giving birth" to the field. An evolutionary approach to explaining variation among individuals in traits such as mate preferences, marriage patterns, and childbearing—or even differences in hunting patterns, diet, language, diseases, and personality—has gained popularity in disciplines besides biology, such as anthropology, psychology, and more recently, medicine. This approach has also been applied in economics, where—much as in evolutionary thinking—maximization and self-interest are central concepts. In contrast, sociologists, for example, have traditionally been slower at integrating evolutionary theory into their approach to explaining human behavior. Consequently, scientists applying evolutionary theory to understanding human behavior have backgrounds and training in an extraordinary diverse range of disciplines. They often disagree about how evolutionary theory can be applied to understanding human behavior and how such attempts should incorporate any influence of culture, modernity, inheritance of wealth, and other factors often considered particularly relevant in humans as compared with other species.

This chapter focuses on discussing the success of the behavioral ecological approach in explaining variation among humans. The first part introduces the key approaches and assumptions traditionally used in the study of human behavioral ecology, and lists the main areas of research and their findings. The second part discusses the difficulties and criticism faced by such studies. The third part highlights the recent developments in the field that arose in response to such criticism, and points out the areas in need of further investigation. Finally, although studies on humans suffer from many unavoidable methodological difficulties, the last section highlights the particular benefits that working with humans offers for advancing our understanding of evolutionary processes in general.

1. DEVELOPMENT OF HUMAN BEHAVIORAL ECOLOGY

Human behavioral ecology began by testing predictions formulated largely from optimality theory. *Optimality models* weigh the costs and benefits of alternative traits or behaviors for maximizing fitness and have been successfully used to further our understanding of behavioral variation in other animals (see chapter VII.3). In humans, short birth intervals, for example, could be associated with the benefit of producing many offspring over the limited reproductive life span, but such benefits must be weighed against the costs of short birth intervals to both mother and child in terms of mortality risk. The best (optimal) strategy thus involves a trade-off between such factors to maximize the overall possible number of offspring raised in a lifetime. The approach typically considers human behavior to be highly plastic and likely to produce adaptive outcomes in different environmental settings. Such a black box approach assumes that there is a link between genes and behavior, but the existence of this linkage was for a long time not studied in detail (see chapter VII.1).

In humans, most quantitative data to test the models have been collected studying contemporary "traditional" societies, such as extant hunter-gatherer, agropastoral, or horticultural groups, for example, in southern Africa (!Kung San), Kenya (Kipsigis), Amazonia (Yanomamö; Tsimane), and Tanzania (Hadza) (see Hawkes et al. 1997). Only the hunter-gatherer lifestyle (e.g., that of the traditional !Kung San) is usually, strictly speaking, expected to be similar to that during Pleistocene, when human evolution is thought to have been rapid; however, because of the current rarity of such groups, research has expanded to other populations little influenced by globalization and with "natural" mortality and fertility rates, with the idea that studying such tribal groups is close to studying our ancestors. Thus, the traits that increase reproductive success among the currently living traditional populations have also done so in the past and can inform us about selection pressures operating in past environments. Because of the desire to correlate given traits or behaviors with measures of reproductive success, such as the number of living children or grandchildren, the data analyzed on these populations have largely been correlational in nature; that is, they have involved collection of anthropometric, behavioral, and demographic data on individuals without the possibility—available for other shorter-lived organisms—to conduct experiments.

One of the first areas of focus was research on foraging behavior to show that, on the whole, human foragers select food sources that maximize nutrient acquisition, as predicted by optimal foraging theory. Further research has applied the optimal theory framework to investigating mating patterns (e.g., to test whether females may gain higher fitness by mating with a male who already has a mate), life history variation (e.g., age at maturation and first reproduction, birth spacing, and senescence), and parental investment according to the prevailing social and environmental conditions. Overall, although these studies cannot necessarily show that the traits in question are the products of past selection, they have proven that applying the same framework as scientists working on similar questions in other species can indeed produce convincing support for the tested hypothesis and provide insight into how natural selection maintains variation in the trait.

For example, one of the greatest mysteries in human life history has been the existence of female menopause, a complete and irreversible physiological shutdown of reproductive potential, well before the commonly achieved overall life span in all human populations. This phenomenon is evolutionarily puzzling, because all organisms are predicted to seek to maximize their genes in the following generations, a goal that is normally achieved by breeding throughout life. The problem is that adaptive benefits of menopause are difficult to test empirically, because all women experience it; we will never know whether in our evolutionary past, women experiencing menopause produced significantly more and/or superior offspring than women who continued to reproduce until death. What is better understood, however, is that whatever the cause for menopause itself, the extended life span after menopause gives an evolutionary advantage to women. A woman with genes for living beyond her decline in fertility produces more grandchildren (and hence forwards more genes to the following generation) than a woman who dies at menopause, because postreproductive women can have positive effects on their offspring's reproductive success—they help rear their own grandchildren. Among the Hadza of Tanzania, child weight is positively correlated with grandmother's foraging time (see Hawkes et al. 1998 for details). The presence of a grandmother has also been linked to increases in grandchild survival chances in many contemporary traditional as well as historical populations around the world. Finally, research using data available for farming/fishing communities of eighteenth- and nineteenth-century Finnish and Canadian people has shown that mothers indeed gained extra grandchildren by surviving beyond menopause until their mid-seventies. These data show that life span can be under positive selection at least until this age. This effect arose because offspring in the presence of their living postreproductive mothers bred earlier, more frequently, for longer, and more successfully. Such benefits were not present if the mother was alive but lived farther apart from her adult offspring, which suggests that the findings are not a mere artifact of better overall survival of both grandmothers and grandchildren in some families (see Lahdenperät et al. 2004 for details). An additional discussion of the evolution of menopause in humans can be found in chapter VII.16.

Another main interest in human behavior ecology has been to investigate the effect of environmental conditions on the fitness benefits of different traits. For example, costs of reproduction to females need to be analyzed in relation to the energy budget of the woman: high costs of reproduction do not have the same effects on women who have good diets and low levels of physical activity compared with women in poor energetic condition. Such physiological consequences of reproduction for women with differing food access are well documented in humans. Further evidence that resource availability may affect selection on life history traits in humans comes from studies showing a negative relationship between number of offspring and postmenopausal life span among poor landless women, whereas for wealthier women, the relationship between fecundity and postmenopausal life span is often positive. A negative relationship between fecundity and longevity may therefore be expected in women who owing to multiple pregnancies and breastfeeding pay high costs of reproduction that cannot easily be compensated for by increases in dietary intake and reduction in physical activity. In contrast, wealthier women can more easily "afford" both large family size and long life span. Comparable differences in the costs of reproduction could also be created, for example, by differing amounts of help available from other individuals with raising the offspring, such as partners, grandparents, or other helpers in the nest, that affect the level of investment made by the mother, but few studies have investigated such effects.

2. PROBLEMS AND CRITICISM

The downside of the original focus on traditional populations with high fertility and mortality rates is that sample sizes tend to be limited; groups are rapidly disappearing or are affected by globalization; collection of multigenerational data often essential for addressing evolutionary questions is time consuming or impossible; and ages are merely estimates. Focusing preferentially on hunter-gatherers also ignores the fact that human evolution has been most rapid, in terms of generation-to-generation changes in gene frequencies, since the invention of agriculture. Investigating modern populations is equally interesting, because differences in reproductive and survival rates among individuals still lead to selection favoring certain heritable traits over others, albeit that the alleles being favored might also be influenced by culture (see chapter VIII.10), in particular modern medical care. Moreover, modern populations lend themselves to current genomic and population genetic analyses.

First, recent analyses of the human genome have revealed that human genetic makeup has responded to the domestication of plants and animals and the spread of agriculture; numerous genes have experienced recent positive selection, and overall considerable selection has occurred in the past 10,000 years (see chapter VIII.12 for more details and examples). These results are at odds with the claims that natural selection affecting humans stopped with the spread of agriculture or at least with the recent modernization, and investigating only those humans exhibiting lifestyles comparable to those practiced during the Pleistocene is relevant for understanding human evolution. Clearly, agriculture has been a powerful selection force whose effects should be more rigorously investigated, and the continued evolution of humans should be better documented.

Second, analyses of the human genome have also revealed that significant genetic differences both among and, in particular, within human populations have arisen from recent selection events. Many scientists who apply natural selection to understand human behavior have traditionally been uncomfortable with assigning any role for genes in explaining variation among individuals or populations, perhaps because of social Darwinism and racially discriminatory perspectives on human evolution put forward during the early half of the 1900s (see also chapter VIII.11). In contrast, a modern approach to investigating the role of genes in human behavior should focus on studying the effects of mating and reproductive patterns on genetic variation, and genetic constraints on trait evolvability in different populations, as well as on how the documented selection on traits together with their underlying genetic architecture predict responses to such selection.

Third, early attempts to apply evolutionary framework to contemporary Western populations sparked criticism on the ground that some aspects of the modern industrialized world are too novel, and humans may be responding nonadaptively to them, making studies on adaptive traits in such populations pointless. This view ignores the fact that in both industrialized human societies with easy access to modern contraception and medical care and traditional societies there is a large variance in the reproductive success of both sexes. In other words, although survival to old age is high among all individuals, not everyone has the same family size, and many individuals even forego reproduction altogether. Such a variance provides material to natural selection that will capitalize on any heritable trait variation linked with higher reproductive success. Thus, even if many behaviors in novel modern environments turn out to be maladaptive, the large opportunity for selection coupled with heritable traits linked with differences in reproductive output of individuals might lead to rapid changes in the genetic makeup of the population over generations, and selection against any traits genetically linked to maladaptive behavior, because any genetically variable traits associated with the variance in reproductive success will experience selection and evolution regardless of the mechanism by which reproductive variance is affected. Consequently, while social Darwinism should not be tolerated, the reality that humans can continue to evolve should not be negated. Yet because of the trend in human behavioral ecology to focus on the past, and the previous criticism for using other than hunter-gatherers (or to some extent horticulturalists, agropastoralists, or farmers with high mortality and fertility rates) as model populations, only recently have scientists started investigating the behavior of people living in industrialized societies from an adaptationist viewpoint. Even fewer studies have been undertaken to examine how the modern environment itself continues to fuel evolution by favoring or disfavoring certain alleles of the genes, and how the drastic demographic shifts in many populations to low birth and death rates during the recent centuries has affected the overall opportunity for selection or specific trait selection.

Human behavioral ecologists are also criticized for seeking adaptive explanations for behaviors even when such explanations are unlikely. Such criticism applies to all behavioral ecology, but pointing out flaws and factors not correctly considered in the evolutionary models of behavior is obviously easier when the study subject is our own species. It should, however, be stressed that human behavioral ecologists investigate not only how human behavior “fits” the given environment with adaptive benefits but also how environmental conditions constrain individual success. For example, poor early environmental conditions for developing individuals, such as unfavorable month or season of birth, reduce longevity and reproductive performance, yet women commonly reproduce during such times. Social norms, cultural practices, and traditions often lead to reproductive outcomes that are not necessarily beneficial in terms of evolutionary fitness—the study of cultural evolution represents an entire field of research investigating such topics but is not discussed further in this chapter (see chapter VIII.10 for details). Furthermore, poor dietary intake during gestation that leads to reduced birth weight of babies has been shown to be associated with their subsequent risk of adverse health, age at sexual maturation, ovarian function, and life span, which suggests that poor early-life conditions influence development and produce adverse effects later in life. The implications of such effects for evolutionary processes should be considered in more detail.

3. NEW FOCUS ON EVOLUTION IN THE MODERN SOCIETIES

Recent methodological improvements in the ability to measure selection, heritability, and response to selection in natural populations of animals have inspired many human behavioral ecologists. The central focus of human behavioral ecology has recently begun to shift from asking how the behavior of modern humans reflects our species' historical response to natural selection, to measuring current selection in contemporary populations as well as investigating how that might (or might not) cause evolution. Calculations that incorporate a measure of selection and heritable variation in traits allow us to predict how traits under selection could change over time. Such evolutionary changes in human populations are likely, because natural selection operates on several morphological, physiological, and life history traits in modern societies through differential reproduction or survival, and variation in many of these traits has a heritable genetic basis. This change of focus has led to several important changes in methods and approaches used in the field.

First, the type of information that can be analyzed has become more diverse, allowing researchers to take full advantage of the exceptional data available only for humans. Historical demographers, population geneticists, and evolutionary biologists are making increasingly better use of (*historical*) *population records* of agricultural or industrialized populations. Such data sets have the benefit of large multigenerational samples, although the type of data available is usually limited to demographic information such as births, marriages, reproductive events, and deaths. There have been recent promising attempts to make better use of extremely large and versatile *cohort studies* and *twin registers* collected by epidemiologists and social scientists on representative samples of people living in contemporary Europe, the United States, and Australia. *Medical intervention studies* that have collected long-term data on their subjects (e.g., after supplementing mothers' diet during pregnancy) offer a much-needed experimental framework for human behavioral ecologists. These data sets are only now making their way into evolutionary studies. Many scientists are also beginning to use noninvasive manipulations, especially in questions related to sexual selection and mate choice, but also when studying life history strategies. For example, subjects can be exposed to images ("environment") associated with high versus low mortality risk and then asked questions about reproductive investment intentions and preferences. Primatologists have conducted between-species comparisons across primates to draw conclusions on human patterns, and worldwide ethnographies and encyclopedias provide an opportunity to perform similar tests among the large variety of human societies, too. All in all, humans experience the widest global range of living conditions and lifestyles, from traditional communities to extreme urbanization, and human behavioral ecologists today ought to use a wide selection of study designs and data sources to investigate all these populations from an evolutionary perspective.

Second, the focus on studying microevolution in contemporary populations has made it necessary to reexamine the old assumption among behavioral ecologists that the details of trait inheritance do not seriously constrain adaptive responses to ecological variation. Estimating heritability of human traits is often considered problematic: an estimation of heritabilities and genetic correlations requires large multigenerational samples and sample sizes often not available in traditional anthropological studies. Furthermore, effects of a common environment shared by close relatives, and cultural transmission, can inflate estimates of heritability. Nevertheless, a review by Stephen Stearns and colleagues (2010) of studies investigating heritability of life history and health traits in humans suggested that although the heritability levels vary considerably among traits and among study populations, many human traits, such as age at first and last reproduction, cardiovascular function, blood phenotypes, weight, and height have measurable heritability and will respond to selection if they are not constrained by genetic correlations with other traits. Fewer studies have investigated such genetic correlations between traits (caused, for example, by the same gene affecting variation in several traits), but there is some suggestion that such effects can set genetic constraints on trait evolution in humans. For example, a study using the historical pedigree records available on rural Finnish people showed significant negative genetic correlations between reproductive traits and longevity (see Pettay et al. 2005). The existence of this genetic variation and covariation implies that females who reproduced at faster rates also had genes for relatively shorter life span, supporting the hypothesis that rate of reproduction should trade off with longevity. Overall, investigation of genes underlying behavioral differences is only beginning in humans, but studies so far suggest that detailed knowledge of the genetic architecture and its dynamics with environmental conditions can provide helpful information on the current evolutionary processes.

Third, an increasing number of studies show that both the opportunity for selection (variation among individuals in fitness) and selection on particular traits can be strong in contemporary populations (see, e.g., Courtiol et al. 2012). The important question is, Do these results predict any phenotypic changes taking place in the mean trait values or the genetic makeup of the population over generations? Understanding such responses to selection reveals how the rapidly changing culture, such as medical care, is changing the biology of humans. A recent study by Sean Byars and his colleagues (2009) measured the strength of selection, estimated genetic variation and covariation, and predicted the response to selection for life history and health traits in the current US population. Natural selection appears to be causing a gradual evolutionary change in many traits: the descendants of the study women were predicted to be on average slightly shorter and stouter, to have lower total cholesterol levels and systolic blood pressure, to have their first child earlier, and to reach menopause later than they would in the absence of evolution. A similar study on a preindustrial French-Canadian population found natural selection to favor an earlier age at first reproduction among women, a trait that was also highly heritable and genetically correlated to fitness in this population. Age at first reproduction declined over a 140-year period and also showed a substantial change in the breeding value (part of the deviation of an individual phenotype from the population mean due to the additive effects of alleles), suggesting that the change occurred largely at the genetic level. These studies demonstrate that microevolution might be detectable over relatively few generations in humans. It must, however, also be borne in mind that phenotypic changes may not always provide robust evidence of evolution, as they may not reflect underlying genetic trends. Many traits such as height, weight, mortality, age at first reproduction, and family size have shown strong secular changes during a *demographic transition* (the change from high birth and death rates to low ones as a country develops from a preindustrial to an industrialized economic system) that may mostly be associated with rapid changes in diet, medicine, and contraception availability. Further studies focusing on how selection interacts with changing early and later-life environment of individuals and is associated with changes in specific sections of the genome are thus needed.

4. WHAT CAN HUMAN BEHAVIORAL ECOLOGY CONTRIBUTE TO THE GENERAL STUDY OF EVOLUTION?

Evolutionary studies on humans are said to suffer from many drawbacks compared with investigations on model animals, because the data are "correlational" given the difficulty in conducting experiments, and the study objects are exceptionally long-lived, which complicates the collection of lifelong data in the field. Nevertheless, humans make it feasible to investigate the details of many central questions in evolutionary biology.

Only in humans is it possible to work on databases that contain the lifetime vital records, medical history, and a range of physical and psychological details for up to millions of recognizable individuals that can in some cases be traced back for several generations. Such data sets allow researchers to investigate selection on and evolutionary change in physiological and health-related traits that could never be feasibly collected for any other animal in natural conditions. Moreover, such data sets also allow studies in selection on personality and cognitive abilities, which have become popular among behavioral ecologists working on animals, but in humans these can be explored in greater detail than in other species and can be linked to lifetime reproductive success. Furthermore, huge investments in documenting the human genome shadow those available for most other species, and genetic data are sometimes available alongside historical pedigree data. In addition, ongoing large research programs to unravel developmental origins of health and disease in humans should offer excellent opportunities to investigate the evolutionary implications of interplays between developmental conditions and genetics in a much longer lived species than those studied so far.

Data available on humans also allow investigations of fitness in a more reliable way than is often possible in similarly long-lived other species, or even in short-lived species in the wild. Many registers allow accurately determining the numbers of grandchildren for each individual, and these provide a far better measure of fitness than simply the number of offspring born, given the considerable trade-offs detected between offspring quantity and quality in humans (and likely in many other species, too, in which large parental investment improves offspring survival and mating success). Importantly, population-based registers allow inclusion of those individuals who never reproduce into the calculations of variance in fitness, which appears crucial given that in the past as well as present human populations, a large fraction of each birth cohort fail to contribute their genes to next generation, and selection is often strongest through recruitment differences rather than differences in the family size among those who do reproduce.

Many "natural experiments" also offer opportunities to investigate evolutionary questions. Such events involve well-documented famines such as the Dutch Hunger Winter during the Second World War (see, e.g., Roseboom et al. 2001 for details), sex-ratio biases created by wars, documented long-term year-to-year variation in crop success and local ecology linked with individual fitness data, or large-scale changes in the demographic parameters of the population that have occurred repeatedly across the world but at different periods in different countries.

Given that humans exhibit all mating systems documented in the animal kingdom (monogamy, polygyny, polyandry, and even promiscuous mating; see chapter VII.4), they also offer interesting opportunities for investigating how changes in mating system affect selection. For example, over the reproductive lifetimes of Utahans born between 1830 and 1894, socially induced reductions in the rate and degree of polygamy corresponded to a 58 percent reduction in the strength of sexual selection, illustrating the potency of sexual selection in polygynous human populations and the dramatic influence that short-term societal changes can have on evolutionary processes.

Finally, humans are also exceptional in that it is possible to reliably study individual variation in complex cognitive traits. Researchers have used methodology relying on simple experimental settings to collect quantitative data on traits such as mating preferences, cooperativeness, and personality. Similar studies are virtually impossible to conduct on animals because the methods involve a certain degree of abstraction. For example, the same individuals can be asked to choose between large numbers of fictive alternatives, such as hypothetical partners. These preferences for mate characteristics can then be further compared with real-life partner characteristics, and the ecological and individual causes and fitness consequences of the degree of mismatch between preferences and actual pairings can be examined.

FURTHER READING

Alvergne, A., and V. Lummaa. 2010. Does the contraceptive pill alter mate choice in humans? Trends in Ecology & Evolution 25: 171–179.

Byars, S. G., D. Ewbank, D. R. Govindaraju, and S. C. Stearns. 2009. Natural selection in a contemporary human population. Proceedings of the National Academy of Sciences USA 107: 1787–1792.

Courtiol, A., J. Pettay, M. Jokela, A. Rotkirch, and V. Lummaa. 2012. Natural and sexual selection in a monogamous historical human population. Proceedings of the National Academy of Sciences USA 109: 8044–8049

Dunbar, R., L. Barrett, and J. Lycett. 2005. Evolutionary Psychology: A Beginner's Guide. Oxford: OneWorld.

Hawkes, K., J. F. O'Connell, N. G. Blurton Jones, H. Alvarez, and E. L. Charnov. 1998. Grandmothering, menopause, and the evolution of human life histories. Proceedings of the National Academy of Sciences USA 95: 1336–1339.

Hawkes, K., J. F. O'Connell, and L. Rogers. 1997. The behavioral ecology of modern hunter-gatherers, and human evolution. Trends in Ecology & Evolution 12: 29–32.

Lahdenperä, M., V. Lummaa, S. Helle, M. Tremblay, and A. F. Russell. 2004. Fitness benefits of prolonged post-reproductive lifespan in women. Nature 428: 178–181.

Laland, K. N., and G. R. Brown. 2011. Sense and Nonsense: Evolutionary Perspectives on Human Behavior. 2nd ed. Oxford: Oxford University Press.

Moorad, J. A., D.E.L. Promislow, K. R. Smith, and M. J. Wade. 2011. Mating system change reduces the strength of sexual selection in an American frontier population of the 19th century. Evolution and Human Behavior 32: 147–155.

Pettay, J. E., L.E.B. Kruuk, J. Jokela, and V. Lummaa. 2005. Heritability and genetic constraints of life-history trait evolution in preindustrial humans. Proceedings of the National Academy of Sciences USA 102: 2838–2843.

Roseboom, T., J. van der Meulen, C. Osmond, D. Barker, A. Ravelli, and O. Bleker. 2001. Adult survival after prenatal exposure to the Dutch famine 1944–45. Paediatric and Perinatal Epidemiology 15: 220–225.

Stearns, S. C., S. G. Byars, D. R. Govindaraju, and D. Ewbank. 2010. Measuring selection in contemporary human populations. Nature Reviews Genetics 11: 611–22.