HUMAN EVOLUTIONARY DEMOGRAPHY

EDITED BY
OSKAR BURGER, RONALD LEE AND REBECCA SEAR

https://www.openbookpublishers.com

Cover image: Ryota Nagasaka. Street Photography, April 20, 2020, https://unsplash.com/photos/w_5TUm7Xa00

Cover design: Jeevanjot Kaur Nagpal

8. Why Do We Do What We Do? Analysing the Evolutionary Function of Reproductive Behaviour

Ruth Mace

In this chapter, I describe the reasoning behind dividing explanations for the evolution of behaviour into four different levels: two proximate explanations relating to mechanism and development; and two ultimate explanations relating to evolutionary history and function. I outline the basic methods we can use to test functional hypotheses about the evolution of behaviour. I note that in natural populations, we often find ourselves studying proximate mechanisms even if our central interest is evolutionary function. I conclude that a distinction between proximate and ultimate explanations for behaviour can be a useful heuristic tool in many situations, even if, in some real-world studies of human behaviour; this distinction is sometimes blurred.

Proximate and Ultimate Questions About Behaviour

How to ask questions about the evolution of behaviour is not quite as simple as it may appear. Social scientists and evolutionary biologists have been arguing about this for some time. Even evolutionary biologists only formulated a framework with which to have these kinds of discussions back in the 1960s, when Ernst Mayr (1961) made a crucial distinction between questions that relate to mechanisms and those that relate to evolutionary function. A couple of years later, Dutch ethologist Niko Tinbergen published a paper on his "four whys" (Tinbergen, 1963), which broke down the categorization of why animals (or humans) do what they do further. He identified mechanistic and development explanations as two "proximate" questions — the how questions. Evolutionary history and evolutionary function were what are usually described as "ultimate" explanations — the why questions. Evolutionary function is how a behaviour contributes to the Darwinian fitness of an organism; that is how it contributes to either or both of survival and reproduction. It involves identifying the fitness costs and benefits of behaviours, and is central to the interests of behavioural ecologists, including those studying human behavioural ecology (HBE). Tinbergen's insight helped everyone, in biology at least, to clarify what kind of evolutionary question they were asking. The understanding that these questions are not mutually exclusive obviates the need to argue about whether proximate or ultimate explanations are the correct ones.

So, for example, why does the baby cry? Because she is hungry (mechanistic); because crying is an innate behaviour that babies do not need to learn (developmental); because all primates have some kind of distress call (phylogenetic); because it makes her mother feed her more, so

she is more likely to survive (evolutionary function); all are potentially correct answers. Actually, the last question on evolutionary function can be unpacked further. There are a number of more precise reasons as to why, in the sense of evolutionary function, a mother might respond to a crying baby by feeding or holding her infant more; these include the possibility that the infant is manipulating the mother, or that she is signalling her vigour to discourage her mother from infanticide (Lummaa, Vuorisalo et al., 1998). There is a surprisingly complex literature on the evolution of begging in chicks in a nest, because the theoretical underpinnings of parent-offspring and sibling conflict can all shape which patterns of offspring begging for food will be favoured by natural selection.

Although Darwin had considered functional explanations for behaviour in depth in his works, ethologists in the twentieth century largely ignored much of his theory of how adaptation arose by natural selection, preferring to focus mainly on proximate explanations for behaviour (many with a particular interest in the developmental questions of nature vs. nurture). However, this did not prove to be a particularly fruitful line of enquiry. It was only after Tinbergen's contributions in the sixties, and E. O. Wilson's textbook on sociobiology in 1972 (Wilson, 1980), and then Krebs and Davies' first textbook on behavioural ecology in 1976, that the fields of sociobiology, and then behavioural ecology were born (Laland and Brown, 2002). Behavioural ecologists have rapidly grown in number since that time, and the scientific agenda began to swing firmly towards trying to understand the evolutionary function of behaviour. Behavioural ecologists developed a strong tradition of developing functional hypotheses and testing them through detailed empirical studies of animals in their natural habitats. The application of this functional thinking to human behaviour and culture was appreciated almost from the beginning (Chagnon and Irons, 1979).

Human evolutionary demography is that part of human behavioural ecology that relates to demographic phenomena. Demographers interested in the "ultimate" evolutionary function of behaviour relating to timing and investment in reproduction, growth and survival are basically studying what evolutionary biologists call life history theory. This is a framework that formalises which combination of life history traits can maximize the lifetime reproductive success of an organism. What is the optimal speed to grow at? When is it optimal to start or stop reproducing? When to die? All of these are questions that are answerable, in theory, if we only knew enough about the environment in which an animal or human lives, and the impact of that environment on its chances of survival and reproduction. These life history traits are all influenced by natural selection in somewhat predictable ways (Roff, 1992). An especially important variable in nearly all these life history questions is the risk of extrinsic (unavoidable) mortality at each life stage. When mortality risks in the environment are high, selection favours a "fast" life history, in which it usually pays to mature as soon as possible, and give birth to a large number of offspring in the hope that some offspring get through and breed themselves before death takes them. Only when extrinsic mortality rates are lower can "slow" life histories, favouring a high level of investment in each of a small number of offspring over a long lifespan, win out, in fitness terms, over the more productive strategy.

Testing Hypotheses About the Ultimate Function of Behaviour

How do we test whether any particular functional hypothesis is correct? There are actually several tools from behavioural ecology at our disposal (Krebs and Davies, 1993). Firstly, of

course, the hypothesis has to be formalised. A verbal model may suffice, but usually evolutionary hypotheses can be modelled formally, to generate qualitative and quantitative predictions. The currency of such models is either Darwinian fitness, or some proxy measure that is thought to correlate with Darwinian fitness (perhaps calories obtained, or babies born that survived). It may also be necessary to include constraints (which may be trade-offs) within the model. In an ideal world, the model is formulated, tested against data, and, if found wanting, our hypothesis can be updated in the light of the empirical evidence.

The simplest method of testing an evolutionary hypothesis is inference from design. This is a weak method, but it is widely used in many areas of evolutionary biology and anthropology. If wings look like they are useful for flying they probably are, and it may not seem to be necessary to design an experiment to test that. But this can lead to "just-so stories" — named after Kipling's fantastical tales — stories that make a kind of sense but are not scientifically formulated, and for which there is no particular evidence! Such storied are untested, and of little use. Therefore, the more formal, quantitative models that can generate more precise and testable predictions are far preferable. There are three main mechanisms for testing these evolutionary hypotheses about function. These are: experimentation, comparative studies comparing individuals within populations and comparative studies across populations or across species.

Experiments

Experimental manipulations are what, ideally, we would like to do to understand evolutionary processes. However, experimentation that influences the reproductive success of real people is usually not possible in human populations, for obvious ethical reasons (plus humans have a very long generation time). We can seek natural experiments, such as political changes or ecological disasters that have happened to influence part of a population and not another part. For example, we compared one area of rural Ethiopia where water supply was improved and another where it was not, and found that the resulting decrease in the energy that women had to spend on collecting water had the effect of decreasing mortality, and increasing their fertility rate (Gibson and Mace, 2006). It also increased infant malnutrition, unexpectedly.

Another example that could be considered a "natural experiment" is the imposition of child policies in China that have forced individuals to severely restrict their fertility since the 1980s, and also the invention of prenatal gender testing, which led to dramatic changes in sex ratios in some parts of Asia (Hesketh and Xing, 2006). Such accidents of history were used to help us understand the nature of sex-biased parental investment, albeit not necessarily in an explicitly evolutionary context. A jump in sex-biased abortions in Asia showed us how behaviour can be apparently maladaptive in the evolutionary sense, at least in the short term; every baby has one mother and one father so a male bias in the sex ratio caused by female infanticide or prenatal sex-specific abortion will actually favour the Darwinian fitness of female children and damage the fitness payoffs from boys, as they became the sex less likely to find a mate in future years. The recent relaxation of the China's one-child policy also provides opportunities for understanding reproductive decision-making in evolutionary contexts (Liu, Duan et al., 2017). Such recent changes can only really tell us about proximate mechanisms in reproductive scheduling, although we may then use inference from those mechanisms to better understand the evolutionary underpinnings of the system.

Comparing Individuals Within Populations

Often, natural variation in a population can help us to infer the causes of fitness differences, which itself gives strong clues about function. For example, a range of predictions regarding the evolutionarily-informed predictions on the effects of sex ratio on divorce, parental investment and risk taking are now being tested on the basis of historical and natural variation in sex ratios across a range of populations where enough data is available (Grosjean and Brooks, 2017, Schacht, Kramer et al., 2017; Uggla and Mace 2017). Such tests are not as powerful as a real experiment (that might include randomisation and careful controls in populations where sex ratio was and was not manipulated, but would obviously not be possible). However, because such comparisons of naturally occurring variation between individuals and within populations directly concern reproductive success, they are getting close to directly testing functional hypotheses. Longitudinal demographic data is especially useful for this task. In the case of the evolution of menopause and post-reproductive life, longitudinal demographic data has been used to show that those children with grandmothers survive better (Sear, Steele et al., 2002), and that those individuals who survive to be old enough to become grandmothers have higher lifetime reproductive success than those that do not (Lahdenpera, Lummaa et al., 2004).

Of course, there are possible confounds, as correlation does not mean causation. It is possible that only high-quality mothers live long enough to become grandmothers (where "quality" is a technical term used in evolutionary biology as shorthand for features that promote survival or reproduction); therefore, whilst it appears that grandmothering enhances a woman's inclusive fitness, actually having a grandmother may not be causing grandchildren to survive; it may be simply that those women who survived into grandmotherhood were those who were the strongest mothers in the population throughout their earlier life and who gave birth to the most surviving offspring. A third variable (such a household wealth or immunity to disease) could explain both variation in offspring number and mother's longevity, resulting in what is known as a "phenotypic correlation". Such phenotypic correlations are the bane of those testing hypotheses about evolutionary function in natural populations. The evidence is more convincing that menopause, or at least post-reproductive lifespan, has to be about grandmothering when it is shown that only those grandmothers living near to their grandchildren had a positive effect (Engelhardt, Bergeron et al., 2019).

A more formal approach to examining variation between individuals within one population is to test to what extent observed phenomena fit the predictions of a mathematical model that optimises reproductive success. Sometimes a verbal model is not precise enough to isolate complex life history trade-offs, and a formal optimality model is required. Life history theory, as mentioned above, concerns how the timing of events such as birth and death, as well as growth, can maximise reproductive success. A model of an optimal life history ideally encompasses all the costs and benefits of certain actions across an entire lifetime, taking into account any constraints that may be relevant. A change in the risks or benefits at one point in the life cycle can alter optimal decisions at another point in the life cycle, making the optimal strategy hard to compute. It could be very specific to a particular environment, making generalisations difficult. Optimality models have been used to address issues of human family size, going back to Blurton-Jones's early analysis of birth intervals in !Kung hunter-gatherers (Blurton-Jones, 1986); this drew on insights from ornithologist David Lack's work on optimal clutch size in passerines (Lack, 1954). Blurton-Jones calculated that short interbirth intervals

increased infant mortality, but there was a trade-off, as very long birth intervals lower lifetime fertility. He calculated that the best trade-off between infant mortality and lifetime fertility (i.e. the decision that maximised lifetime reproductive success or LRS) was for !Kung mothers to have a baby about every four years (Blurton-Jones, 1986). This did represent the median birth interval observed by Nancy Howell's demographic data from this foraging population. Thus, he concluded that the ultimate explanation for !Kung long birth intervals is to optimise the fertility/infant mortality trade-off and thus maximise LRS.

He hypothesized that the proximate mechanism that drove birth spacing was the energetic costs suffered by mothers who had to carry two young infants at the same time (as well as any food they had gathered and wanted to take to camp), which he called the "back load model". The proximate explanations for these long birth intervals were that the energetic burden of carrying and breast-feeding any infants caused lactational amenorrhea, and that cultural taboos against resuming sexual activity for a couple of years after giving birth help to space births, and hence helped to reduce the mortality that would arise from shorter interbirth intervals. Interestingly, those !Kung who settled in cattle camps, giving up their nomadic lifestyle, did not suffer such high energetic costs of child care, as they could leave children in camp; so they had fewer constraints, and their birth intervals shortened. Whether this might in fact also be due to other factors such as increased food supply or a reduced burden of sexually transmitted infections is not entirely clear (Pennington, 1992).

One of the problems with a simple model predicting a single optimum, as in the birth interval example just given, is that real data displays an array of birth intervals. Why do some women consistently reproduce too fast or too slowly to optimise that predicted LRS? There are many important reasons — and deviation from a simple model can help us identify them. The process of science in general, and behavioural ecology in particular, works by proposing simple models and rejecting those aspects that fail to predict the data; then going back and improving the model to help us to understand the system better. Women may all have different optima based on their own individual costs of reproduction, as mentioned above; or, women may fail to reach their optimum due to constraints.

Optimality models do have to take constraints into account. Many of the debates in evolutionary demography concerning apparently maladaptive behaviour revolve around whether or not a behaviour is the result of hidden costs and benefits or simply constraints (cognitive, behavioural, physiological or time constraints). For example, some have argued that the span of primate female fertility (including in humans) is constrained to a maximum age of about fifty years, so no functional explanation for menopause is required (Kim, Coxworth et al., 2012). Others, including myself, disagree, but unfortunately the testing of hypotheses about constraints is rather hard. Resorting to the argument that evolution simply cannot solve certain problems can shut down the evolutionary debates, as it is hard to prove a negative. Failure to find a mate or infertility caused by an STI could constrain female fertility below the optimum in individual cases. But constraints seem unlikely to provide a satisfactory explanation for population-wide or species-wide phenomena like menopause, or the demographic transition to low fertility.

Lack of control over decision-making could also push fertility above the optimum, as might be the case in some societies where there is a conflict of interest between male and female optimal fertility, with males paying lower costs of high fertility than do females, and thus

favouring faster reproduction and perhaps not observing adequate post-partum sexual taboos. Females may have to bow to male optima if they do not have bargaining power.

This may apply in the Dogon in Mali, where rates of polygynous marriage and high fertility appear to be associated with high infant mortality and are not beneficial for female reproductive success (Strassmann, 2011).

Alternatively, the diversity may reflect phenotypic variation in female quality, or variation in other aspects of her state (such as whether she has help from allocarers). Simple optimality models effectively assume everyone is the same. However, some mothers have physiological or social advantages that will enable them to reproduce at a much higher rate than others without much increase in mortality risk. Each mother has her own optimum, depending on her state, with the result that most data on birth intervals reveals that those mothers with the highest birth rate usually have the highest reproductive success. This does not mean there are no trade-offs; it is simply that we may not see them because phenotypic correlations are also present. High-quality mothers are more successful than low-quality mothers. Experimental studies in birds, where the number of eggs in the nest can be manipulated experimentally, so that clutch sizes are random with respect to female quality (Gustafsson, 1994), do reveal these correlations. Humans obviously cannot be manipulated in the same way. Of course, chance events (in each individual history) can also generate variation — mortality, for example, is highly stochastic.

A more realistic and powerful framework for modelling optimal reproductive decision-making is stochastic dynamic programming, in which reproductive success over the lifetime is modelled, in a stochastic environment and where decisions are state-dependent (Houston, Clark et al., 1988). This is, of course, much more realistic. For example, birth rates depend on the characteristics (state) of both the woman herself and of the family (environment) that each woman finds herself in. Whether or not it is optimal to have another baby could depend on many features of the mother's current state, such as when her last birth was, did the child survive, the size of the family and how much food or other resources are available. Dynamic programming of such decisions has been used to model reproductive scheduling in the !Kung, enabling the risk of mortality for both mother and infant to be included, and the model generated realistic reproductive schedules (Anderies, 1996).

The same approach was used to see how wealth and the sex of the existing offspring, as well as mortality risks, influenced optimal reproductive scheduling in the Gabbra, who are camel pastoralists in Kenya. Here, most of the costs of setting up offspring in their own new families fell onto the parents of sons (Mace, 1998). Decisions to reproduce depended on wealth and the number of sons a family already had. The model showed that mortality risk had little influence on optimal family size but had a large influence on the number of births (as it is optimal to quickly "replace" births when the infant does not survive, but the higher mortality balances out the effect of the higher birth rate generating little effect on final family size). The model further showed that marriage costs (bride price) also had a big influence on optimal reproductive decisions, with smaller family sizes becoming optimal when marriage costs were high. This optimality framework shows how high costs of raising children co-evolve with low fertility.

Thomas et al. used this approach to investigate the relationships between sibling helping and sibling conflict, and their effect on birth intervals (Thomas, Shanley et al., 2015); they show that sibling competition and mortality risk interact, in that sibling competition only has a serious influence on optimal birth intervals when mortality is low. This captures one of

the essential features of the demographic transition to low fertility, which is that, as mortality has declined, parents appear to invest more in each offspring at the expense of high fertility (a trend that has occurred worldwide over the last 200 years). This model also showed that these factors alone, which only considered the two generations of parent and offspring, could not generate the evolution of menopause. The current evidence suggests that any model that predicts the evolution of menopause requires the inclusion of the grandparental generation and grandmother benefits in its evolutionary dynamics (Thouzeau and Raymond, 2017). This study examines the evolutionary dynamics of menopause, hence addressing both the selective forces that maintain it and those that drive its evolution in the first place, showing that the important selective pressures at these two levels of explanation can differ.

Comparison Across Different Populations

One important way to test hypotheses about how the risk of mortality shapes animal behaviour is comparison across species. This is widely used to test hypotheses about evolutionary history and function in biology. If species living in certain environments are more likely to do one thing than another, then a statistical case can be built for a functional association (in Tinbergen's sense of "why did natural selection favour that?"). For example, testes size is a measure of a mating system, as it is reveals how important sperm competition is. Sperm competition occurs when females mate with several males, and, in circumstances where males cannot prevent this by mate guarding, their best chance of being the one that fertilizes the egg lies in delivering a large amount of sperm with each mating. Chimpanzees (*Pan Troglodytes*) have huge testes by comparison with humans, telling us instantly that rates of female polyandrous mating (females mating with multiple males) are much higher in chimps than in humans (Harcourt, Harvey et al., 1981). In gorillas, however, where males tend to have little competition for access to females in their family groups, testes are small. Human testes are small compared to chimps, but slightly larger than gorillas, suggesting we are only a mildly polygamous species. This fits with the observed patterns of marriage norms cross-culturally, where some form of polygynous marriage is the most common marriage system, and even in human populations in which marriage is monogamous, serial monogamy is common (Murdock, 1967). In theory, were we to discover a new ape species previously unknown to science, we could immediately guess something about the mating system of this new species based on physiology alone.

Although there used to be quite a range of human-like sister species or ancestors, *Homo sapiens* (ourselves) is the only human species that remains extant. Life history does not fossilize well, so comparison across very closely related species is not really possible in the hominin line. However, we can do comparative studies across human cultures. Languages rarely hybridize and thus can act as badges of demarcation, broadly dividing the world into ethnolinguistic groups. Such groups often have different cultural norms with respect to customs such as mating system, marital and residence arrangements, the role of women, who cares for children and who works in the fields or contributes to other forms of subsistence, whether there is warfare within or between groups. These variables can all generate different demographic profiles.

We can borrow statistical tools from evolutionary biology to try to clarify the evolutionary processes that have given rise to this variation (Pagel, 1999; Mace, Holden et al., 2005). Phylogenetic comparative methods are powerful and accurate for trying to understand evolutionary processes. They can be used to infer ancestral states from data on extant cultures

or species (in this case cultures), if we have information with which to map the evolutionary relationship between these groups (cultures) onto phylogenetic trees. In cross-cultural studies, these phylogenetic trees map the historical relationships between ethnolinguistic groups through linguistic similarity, as words have the properties of a culturally transmitted replicator (Pagel, 2009). Because cultures usually mix to some extent through migration and intermarriage, the genetic history of neighbouring groups is not necessarily very tree-like. However, languages do not usually blend in the way that genetic material does. Children of mixed parentage with respect to language tend to learn the dominant language of their population, or both languages, but not a blend of the two. This has meant that languages retain signals that can be used to infer cultural historical relationships.

This not to say that words are never borrowed. Clearly many of them are, especially when the beliefs or technology that those words refer to are also borrowed; but on the whole the strong frequency-dependent nature of linguistic communications means that differences in core vocabulary can usually be very helpful for inferring phylogenetic trees of culture (Mace, 2005). Statistical methods can then use a combination of the phylogenetic tree, and the data on the extant cultures that we observe, to infer what cultural states may have looked like at various nodes on the tree that represent ancestral cultures (Pagel, 1999). Anthropology is generally confined to the present, but these methods for estimating ancestral states potentially enlighten us as to the likely patterns in prehistory that led the past to generate the diversity that we see in the present.

Phylogenetic comparative methods are just statistical approximations of course, and as with all statistics, and all science, the conclusions are only as good as the data and the assumptions on which they are based. However, they do provide a principled and repeatable scientific framework within which to ask questions such as: what were the ancestral states of certain cultural traits? What were the rates of evolutionary change in each direction? Does one cultural trait co-evolve with another cultural trait, or with a particular feature of the physical environment? What was the most likely order in which two traits evolved over time? These are especially important questions for understanding evolutionary function, because the co-evolution of two traits in cultures that have ancestral relationships is almost impossible to infer unless the phylogenetic relationships are known (Mace and Pagel, 1994). Uncertainty in phylogenetic trees, and in the path of evolution along the branches of those trees, can now be estimated using a range of Bayesian phylogenetic comparative methods (Huelsenbeck, Ronquist et al., 2001; Pagel, Meade et al., 2004; Pagel and Meade 2006). Hence, phylogenetics is very important with respect to both of the two "whys" that Tinbergen described as ultimate: function and evolutionary history. Ancient DNA is another technology that is generating a lot of tangentially relevant information on our recent (i.e. from the last 10,000 years) prehistory, and that will help to inform our knowledge of some (but of course not all) aspects of prehistoric populations and their movements, which will constrain and improve cultural phylogenetic models. The prospects of understanding our cultural evolutionary history are thus improving all the time.

One simple example of this approach, relating to human social organisation, is the evolution of matrilineal kinship (where names and property are inherited down the female line). Anthropologists had long noted a correlation between cattle keeping and patrilineal social organisation in Africa (Aberle, 1961). This example used a method borrowed from evolutionary

biology, designed to investigate the co-evolution of two discrete traits (Pagel, 1994) (in this case matriliny/patriliny and cattle/no cattle). There are examples of Bantu cultures in all four of the possible resulting combinations of presence/absence of cattle and presence/absence of matriliny. Phylogenetic methods, based on a language tree of the Bantu-speaking populations, were used to show the likely directions of such changes, and thus help test the hypothesis that the adoption of pastoralism generated patriliny (Holden and Mace, 2003). It is possible to test whether the state of one variable influences the rates of change in another (Pagel, 1994). Analyses showed that transitions between all of the four different states occurred and could go in all directions, but some transitions are more likely than others. In populations without cattle, transitions between matriliny and patriliny were quite common; but, once a population adopted cattle, a combination of cattle keeping and matriliny was very unstable, and transition rates out of that state were high. In contrast, pastoralism combined with patriliny is a much more stable and consistent state, with high rates of transition into it and low rates of transition out of it. Note that it was unlikely, however, that patrilineal groups without cattle then acquired cattle to become patrilineal groups with cattle; an evolutionary pathway via an intermediate matrilineal state appears to have been more common (at least in Africa, where the data for this study were from).

Phylogenetic comparative methods can also be applied to understanding the evolution of quantitative rather than discrete traits (although such methods are not quite as powerful with regard to understanding evolutionary history as they do not involve an explicit evolutionary model of the direction of change). Sex ratio is one example of a quantitative trait that has been examined in this way, using comparisons across Old World human cultures (Mace and Jordan, 2005). As language trees are only good at inferring relationships within language families, and less good at deeper historical relationships (as signal tends to be lost after about 10,000 years of time depth), a genetic tree was used in this case. Sex ratio at birth did not correlate with sex ratio in adulthood. Male-biased adult sex ratios (which may reflect higher female mortality) appear to be associated to some extent with bride price (that is a transfer of resources at marriage from the family of the groom to the family of the bride) across cultures. Hence in cultures where there is heightened competition between males for scarcer females, parents of girls are enabled to demand bride price. Other demographic traits that have been the subject of hypothesis testing, using various phylogenetic comparative methods, include correlations between social structure and the evolution of post-reproductive life across mammals (Nichols, Zecherle et al., 2016). Some models of the grandmother hypothesis for menopause argue that competition between generations of females for reproductive resources in communally breeding species (like humans) is more intense in patrilocal species, where females disperse at reproductive age and are therefore not related to each other (Johnstone and Cant, 2010). Other models argue that genomic conflict will result in worse menopause symptoms in matrilocal groups where females compete with their own relatives (Úbeda, Ohtsuki et al., 2014). However, there is no evidence from comparison across patrilocal and matrilocal cultures that either the timing of menopause or the severity of symptoms fits either of these models in human cultural groups (Snopkowski, Moya et al., 2014; Yang, Arnot et al., 2019). Yang et al. (2019) actually found worse menopause symptoms in patrilocal (female dispersing) groups, contrary to the predictions of the genomic conflict model.

Proximate and Ultimate Revisited?

The methods I have described for testing the function of aspects of human behaviour, be they reproductive scheduling or social organisation, are borrowed, perhaps with some modifications, from those methods used by behavioural ecologists and evolutionary biologists studying natural diversity in a range of species. If we are using cultural groups for comparison, that means that we are most likely studying the evolution of variation in cultural traits that are socially transmitted and inherited, rather than genetic traits; this is known as cultural evolution, or gene-culture evolution in some cases. (The definitions of cultural evolution are various, but one of the most common definitions of a cultural trait is just a trait that is transmitted socially; however, this is of little use in human studies as almost all traits fall into that category). There has been some debate as to whether those of us studying cultural evolution are studying proximate mechanisms or ultimate function. Those who have defined themselves as human behavioural ecologists, such as myself, tend to use the methods of behavioural ecology described above to study what we consider to be the functional basis of human behavioural and cultural diversity. We often seek patterns of natural or experimental variation that fit the predictions of an optimality model or other hypothesis, paying less attention to the proximate mechanism that drove that behaviour to develop. It is enough to concentrate on the phenotype and its distribution in nature or society. Diversity in human norms of behaviour is usually learnt, so much of it is usually best thought of as cultural in origin. In that sense, I do not consider studies in human behavioural ecology and in cultural evolution to be very different (Mace, 2014). The phylogenetic comparative study of matriliny and pastoralism just described, for example, can clearly be understood as a study in both cultural evolution and human behavioural ecology.

Studies of evolutionary dynamics, such as those considering how different selective forces or transmission probabilities of cultural traits lead to certain attributes emerging, may be hard to describe as proximate or ultimate explanations. Such models are similar to population genetic models, but focus on cultural rather than genetic traits. They may fit better into Tinbergen's more specific category of evolutionary historical explanation. For example, if populations adopt matrilocal residence and dispersal patterns when those around them are matrilocal because it enhances reproductive success, as we have shown that they do in southwestern China (Ji, Zheng et al., 2016), then I am happy to describe that as a functional explanation, or an evolutionary explanation. However, it is true that no gene frequencies are necessarily altered in this case; the decision by human females to disperse or not to disperse is almost certainly culturally inherited, so only the frequency of cultural traits change. Describing a study or model of mechanisms of transmission as revealing the ultimate function of cultural behaviour traits is not uncommon, as some like to describe transmission mechanisms as determining "cultural fitness". Some have argued that the proximate ultimate dichotomy is not helpful when thinking about certain aspects of cultural evolution in particular, including niche construction (where man-made environments feed back on the selective pressures imposed on future generations) (Laland, Sterelny et al., 2011). West and others have characterised this as an error, a confusion of Mayr's original distinction between proximate and ultimate causation (West, El Mouden et al., 2011). This is probably just a semantic debate, albeit one that has generated some heat. West et al.'s paper met with some hostility on one side, and the news that the Templeton Foundation was pouring a large amount of money into a grant to investigate the need for a new and "extended evolutionary synthesis" met with a somewhat incredulous reaction on social media

on the other side. These are surprising levels of hostility for fairly arcane matters of academic definition.

Definitions are only useful as tools to help understanding. Proximate determinants of reproductive rate are the usual fare of demographic papers, be they aimed at testing evolutionary hypotheses or not. If the proximate/ultimate distinction helps understanding in evolutionary demography, and if its blurring leads to more potential misunderstandings between biologists and social scientists, then these definitions need to be maintained when it is useful to do so. The study of cultural evolutionary processes is not belittled by such processes being described as proximate mechanisms. However, if the distinction is causing confusion with respect to cultural evolutionary models, which look at the dynamics of changes in frequencies of cultural traits in populations, then Tinbergen's full four questions may be needed to avoid confusion. Such models describe the likely evolutionary pathways that drive certain patterns to emerge (evolutionary history). Such models are undoubtedly evolutionary, even if the words "functional" or "ultimate" do not always readily describe these cultural processes.

Thinking about the evolutionary implications and the function of reproductive patterns of behaviour can help set research agendas. The role of grandmothers in childcare, for example, was a minority interest amongst only very few demographers. However, once Hawkes and others had stressed its potential role in the evolution of menopause (Hawkes, O'Connell et al., 1998), the number of studies of the effect of grandmothers and all other kin on child survival, adult reproduction and a range of other outcomes, like education and health, mushroomed, partly by bringing a new breed of researchers from other fields into the study of large demographic databases. Evolutionary function remains an intriguing research framework on which to hang our continued efforts to work out why people do what they do in all realms of our behaviour, including our demography.

Acknowledgements

References[1]

Aberle, D. F. 1961. 'Matrilineal descent in cross-cultural perspective', *Matrilineal Kinship*, ed. by D. M. Schneider and K. Gough (Berkeley: University of California Press), pp. 655–727.

Anderies, J. M. 1996. 'An adaptive model for predicting !kung reproductive performance: A stochastic dynamic programming approach', *Ethology and Sociobiology*, 17.4: pp. 221–45. https://doi.org/10.1016/0162-3095(96)00037-4

Blurton-Jones, N. 1986. 'Bushman birth spacing – a test for optimal interbirth intervals', *Ethology and Sociobiology*, 7.2: pp. 91–105. https://doi.org/10.1016/0162-3095(86)90002-6

Chagnon, N. and W. Irons. 1979. *Evolutionary Biology and Human Social Behaviour* (North Scituate, Massachusettts: Duxbury Press).

---

[1] Note this chapter has been posted on the Open Science Framework website since 10/04/2020, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

Engelhardt, S. C., P. Bergeron, A. Gagnon, L. Dillon and F. Pelletier. 2019. 'Using Geographic Distance as a Potential Proxy for Help in the Assessment of the Grandmother Hypothesis', *Current Biology*, 29.4: pp. 651–56.e653. https://doi.org/10.1016/j.cub.2019.01.027

Gibson, M. A. and R. Mace. 2006. 'An energy-saving development initiative increases birth rate and childhood malnutrition in rural Ethiopia', *Plos Medicine*, 3.4, pp. 476–84. https://doi.org/10.1371/journal.pmed.0030087

Grosjean, P. and R. C. Brooks. 2017. "Persistent effect of sex ratios on relationship quality and life satisfaction', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372.1729: pp. 20160315. https://doi.org/10.1098/rstb.2016.0315

Gustafsson, L. 1994. 'Infectious disease, reproductive effort and the cost of reproduction in birds', *Philosphical Transactions of the Royal Society London Series B*, 346.1317: pp. 323–31. https://doi.org/10.1098/rstb.1994.0149

Harcourt, A. H., P. H. Harvey, S. G. Larson and R. V. Short. 1981. 'Testis weight, body weight and breeding system in primates', *Nature*, 293.5827: pp. 55–57. https://doi.org/10.1038/293055a0

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*, 95.3: pp. 1336–39. https://doi.org/10.1073/pnas.95.3.1336

Hesketh, T. and Z. W. Xing. 2006. 'Abnormal sex ratios in human populations: Causes and consequences', *Proceedings of the National Academy of Sciences*, 103.36: pp. 13271–13275. https://doi.org/10.1073/pnas.0602203103

Holden, C. J. and R. Mace. 2003. 'Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis', *Proceedings of the Royal Society B-Biological Sciences*, 270.1532: pp. 2425–33. https://doi.org/10.1098/rspb.2003.2535

Houston, A. I., C. W. Clark, J. McNamara and M. Mangel. 1988. 'Dynamic models in behavioural and evolutionary ecology', *Nature*, 332.6159: pp. 29–34. https://doi.org/10.1038/332029a0

Huelsenbeck, J. P., F. Ronquist, R. Nielsen and J. P. Bollback. 2001. 'Bayesian Inference of Phylogeny and Its Impact on Evolutionary Biology', *Science*, 294.5550: pp. 2310–14. https://doi.org/10.1126/science.1065889

Ji, T., X.-D. Zheng, Q.-Q. He, J.-J. Wu, R. Mace and Y. Tao. 2016. 'Kinship as a frequency dependent strategy', *Royal Society Open Science*, 3.2: pp. 150632. https://doi.org/10.1098/rsos.150632

Johnstone, R. A. and M. A. Cant. 2010. 'The evolution of menopause in cetaceans and humans: the role of demography', *Proceedings of the Royal Society B-Biological Sciences*, 277.1701: pp. 3765–71. https://doi.org/10.1098/rspb.2010.0988

Kim, P. S., J. E. Coxworth and K. Hawkes. 2012. 'Increased longevity evolves from grandmothering', *Proceedings of the Royal Society B: Biological Sciences*, 279.1749: pp. 4880–84. https://doi.org/10.1098/rspb.2012.1751

Krebs, J. R. and N. B. Davies. 1993. *An Introduction to Behavioural Ecology, Third Edition* (Oxford, England: Blackwell Scientific Publications).

Lack, D. 1954. 'The evolution of reproductive rates', in *Evolution as a Process*, ed. by J. S. Huxley, A. C. Hardy and E. B. Ford (London: Allen and Unwin), pp. 143–56.

Lahdenpera, M., V. Lummaa, S. Helle, M. Tremblay and A. F. Russell, 2004. 'Fitness benefits of prolonged post-reproductive lifespan in women', *Nature*, 428.6979: pp. 178–81. https://doi.org/10.1038/nature02367

Laland, K. N. and G. R. Brown. 2002. *Sense and Nonsense. Evolutionary Perspectives on Human Behaviour* (Oxford: Oxford University Press).

Laland, K. N., K. Sterelny, J. Odling-Smee, W. Hoppitt and T. Uller. 2011. 'Cause and Effect in Biology Revisited: Is Mayr's Proximate-Ultimate Dichotomy Still Useful?, *Science*, 334.6062: pp. 1512–16. https://doi.org/10.1126/science.1210879

Liu, J., C. Duan and V. Lummaa. 2017. 'Parent-offspring conflict over family size in current China', *American Journal of Human Biology*, 29.3. https://doi.org/10.1002/ajhb.22946

Lummaa, V., T. Vuorisalo, R. G. Barr and L. Lehtonen. 1998. 'Why Cry? Adaptive Significance of Intensive Crying in Human Infants', *Evolution and Human Behavior*, 19.3: pp. 193–202. https://doi.org/10.1016/s1090-5138(98)00014-2

Mace, R. 1998. 'The co-evolution of human fertility and wealth inheritance strategies', *Philosophical Transactions of the Royal Society*, 353.1367: pp. 389–97. https://doi.org/10.1098/rstb.1998.0217

Mace, R. 2005. 'On the use of phylogenetic comparative methods to test co-evolutionary hypotheses across cultures', *The Evolution of Cultural Diversity: A Phylogenetic Approach*, ed. by R. Mace, C. J. Holden and S. J. Shennan (London and Walnut Creek, USA: Left Coast Press), pp. 199–205.

Mace, R. 2014. 'Human behavioural ecology and its evil twin', *Behavioural ecology*, 25.3: pp. 443–49. https://doi.org/10.1093/beheco/aru069

Mace, R., C. Holden and S. J. Shennan, (eds.). 2005. *The Evolution of Cultural Diversity: A Phylogenetic Approach* (University College London and Walnut Creek, USA: Left Coast Press).

Mace, R. and F. M. Jordan. 2005. 'The evolution of human sex ratio at birth: a biocultural analysis', *The Evolution of Cultural Diversity: A Phylogenetic Approach*, ed. by R. Mace, C. J. Holden and S. J. Shennan (London and Walnut Creek, USA: Left Coast Press), pp. 207–16.

Mace, R. and M. Pagel. 1994. 'The comparative method in anthropology', *Current Anthropology*, 35.5: pp. 549–64. https://doi.org/10.1086/204317

Mayr, E. 1961. 'Cause and Effect in Biology', *Science*, 134.3489: pp. 1501–06. https://doi.org/10.1126/science.134.3489.1501

Murdock, G. P. 1967. *Ethnographic Atlas* (Pittsburgh: University of Pittsburgh Press).

Nichols, H. J., L. Zecherle and K. Arbuckle, 2016. 'Patterns of philopatry and longevity contribute to the evolution of post-reproductive lifespan in mammals', *Biology Letters*, 12.2: 20150992. https://doi.org/10.1098/rsbl.2015.0992

Pagel, M. 1994. 'Detecting correlated evolution on phylogenies – a general-method for the comparative-analysis of discrete characters', *Proceedings of the Royal Society B-Biological Sciences*, 255.1342: pp. 37–45. https://doi.org/10.1098/rspb.1994.0006

Pagel, M. 1999. 'Inferring the historical patterns of biological evolution', *Nature*, 401.6756: pp. 877–84. https://doi.org/10.1038/44766

Pagel, M. 2009. 'Human language as a culturally transmitted replicator', *Nature Reviews Genetics*, 10.6: pp. 405–15. https://doi.org/10.1038/nrg2560

Pagel, M. and A. Meade. 2006. 'Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo', *American Naturalist*, 167.6: pp. 808–25. https://doi.org/10.1086/503444

Pagel, M., A. Meade and D. Barker. 2004. 'Bayesian estimation of ancestral character states on phylogenies', *Systematic Biology*, 53.5: pp. 673–84. https://doi.org/10.1080/10635150490522232

Pennington, R. 1992. 'Did food increase fertility? Evaluation of Kung and Herero history', *Human Biology*, 64.4: pp. 497–521. https://www.jstor.org/stable/41464305

Roff, D. A. 1992. *The Evolution of Life Histories* (New York: Chapman and Hall).

Schacht, R., K. L. Kramer, T. Székely and P. M. Kappeler. 2017. 'Adult sex ratios and reproductive strategies: a critical re-examination of sex differences in human and animal societies', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372.1729: pp. 20160309. https://doi.org/10.1098/rstb.2016.0309

Sear, R., F. Steele, I. A. McGregor and R. Mace. 2002. 'The effects of kin on child mortality in rural Gambia', *Demography*, 39.1: pp. 43–63. https://doi.org/10.1353/dem.2002.0010

Snopkowski, K., C. Moya and R. Sear. 2014. 'A test of the intergenerational conflict model in Indonesia shows no evidence of earlier menopause in female-dispersing groups', *Proceedings of the Royal Society B: Biological Sciences*, 281.1788: pp. 20140580. https://doi.org/10.1098/rspb.2014.0580

Strassmann, B. I. 2011. 'Cooperation and competition in a cliff-dwelling people', *Proceedings of the National Academy of Sciences*, 108.Supplement 2: pp. 10894–10901. https://doi.org/10.1073/pnas.1100306108

Thomas, M. G., D. P. Shanley, A. I. Houston, J. M. McNamara, R. Mace and T. B. L. Kirkwood. 2015. 'A dynamic framework for the study of optimal birth intervals reveals the importance of sibling competition and mortality risks', *Journal of Evolutionary Biology*, 28.4: pp. 885–95. https://doi.org/10.1111/jeb.12613

Thouzeau, V. and M. Raymond. 2017. 'Emergence and maintenance of menopause in humans: A game theory model', *Journal of Theoretical Biology*, 430.Supplement C: pp. 229–36. https://doi.org/10.1016/j.jtbi.2017.07.019

Tinbergen, N. 1963. 'On aims and methods of ethology', *Z. Tierpsychol*, 20.4: pp. 410–33. https://doi.org/10.1111/j.1439-0310.1963.tb01161.x

Úbeda, F., H. Ohtsuki and A. Gardner. 2014. 'Ecology drives intragenomic conflict over menopause', *Ecology Letters*, 17.2: pp. 165–74. https://doi.org/10.1111/ele.12208

Uggla, C. and R. Mace. 2017. 'Adult sex ratio and social status predict mating and parenting strategies in Northern Ireland', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372.1729: pp. 20160318. https://doi.org/10.1098/rstb.2016.0318

West, S. A., C. El Mouden and A. Gardner. 2011. 'Sixteen common misconceptions about the evolution of cooperation in humans', *Evolution and Human Behavior*, 32.4: pp. 231–62. https://doi.org/10.1016/j.evolhumbehav.2010.08.001

Wilson, E. O. 1980. *Sociobiology. The Abridged Version* (Harvard, Massachussetts: Belknap & Harvard University Press).

Yang, Y., M. Arnot and R. Mace. 2019. 'Current ecology, not ancestral dispersal patterns, influences menopause symptom severity', *Ecology and Evolution* (in press).