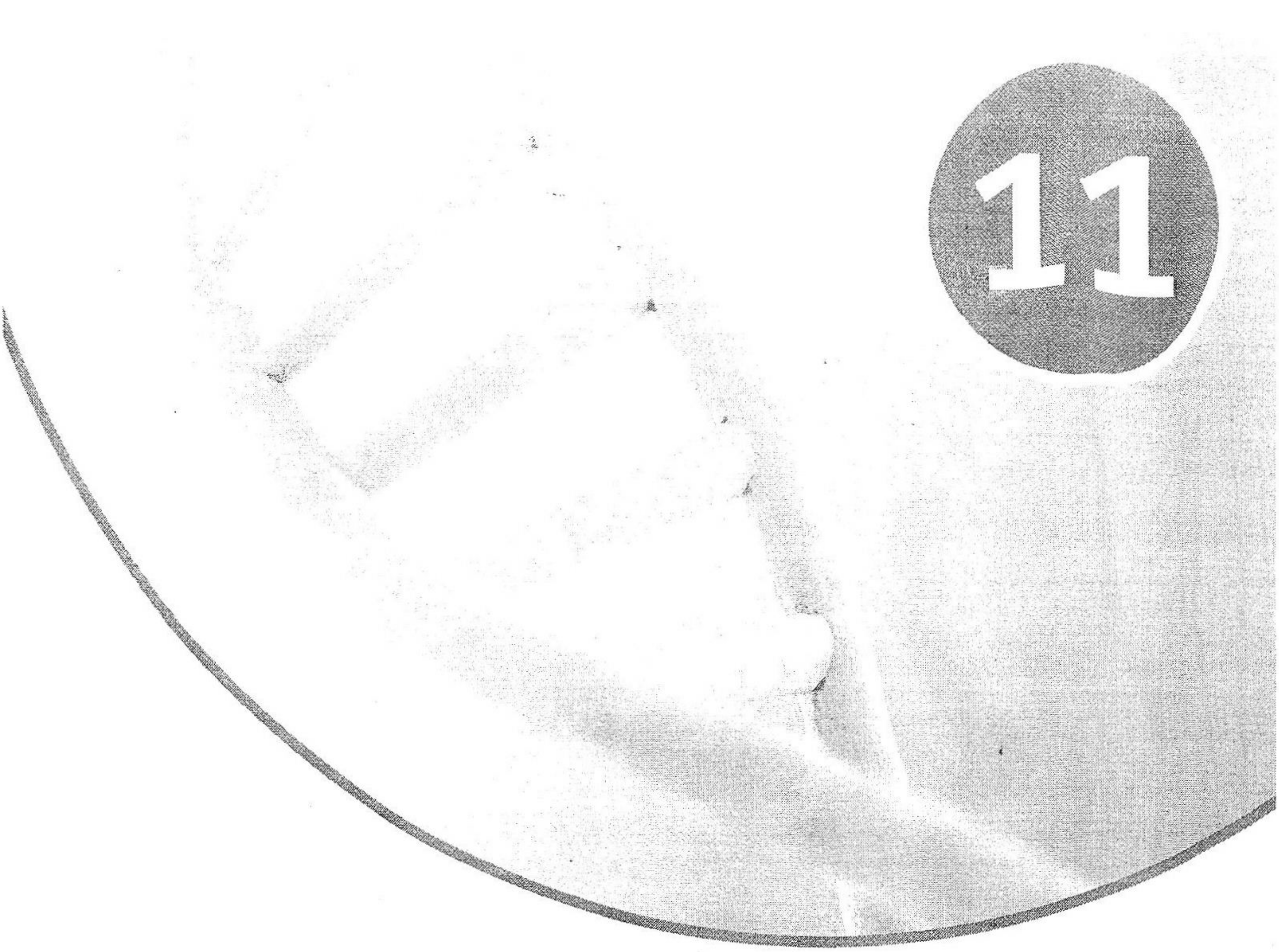


11

Evolution and contemporary life

We have now reviewed all of the areas of evolutionary biology covered by this book. This final chapter asks how what we have learned applies to people living in the contemporary environment. This is an important issue because many researchers in the human sciences accept that human evolution is something that happened, but feel it was all in the past and thus that evolutionary theory offers little insight into why people do what they do now. Needless to say, I see this as a misapprehension and in this chapter I will argue for the value of understanding evolution for understanding the present.

Section 11.1 takes issue with the view that human evolution is something that happened back in the past, by providing evidence that natural selection is still going on. Section 11.2 argues, moreover, that evolution leaves a legacy and contemporary behaviour can never be understood without appreciating this. Section 11.3 considers how evolutionary ideas and understandings fit in with the accounts of human behaviour provided by other psychological, sociological, and anthropological theories that do not make reference to evolution. Finally, in sections 11.4 and 11.5 we conclude by considering two key issues that any adequate human science must provide a good account of: how do we explain cross-cultural variation and how much of our behaviour is adaptive. In doing this, we encounter three of the main contemporary evolutionary approaches to human behaviour: evolutionary psychology, human behavioural ecology, and gene-culture co-evolution theory.

11.1 Human evolution is still going on

It is a strange conceit of human beings to imagine that, having reached their current state, their evolution has stopped. However, we know that this is not so. Not all individuals conceived are equally likely to survive and reproduce, and so natural selection in humans is still going on. Indeed, it may be going faster than in previous ages. There are two main lines of evidence for current selection: evidence from the genome (section 11.1.1) and evidence based on measuring reproductive success at the phenotypic level (section 11.1.2). Finally, one recent study combines evidence from both levels (section 11.1.3).

11.1.1 Ongoing selection in the human genome

At the genetic level, there is very strong purifying selection in force against most new mutations. We know this because a large proportion of all conceptions are spontaneously aborted and this is often because the foetus is carrying some major genetic mutation. In addition, individuals with major mutations often have Mendelian diseases, which impair survival or reproduction. However, purifying selection only maintains the status quo and there is strong evidence that directional selection is also at work in humans.

Most genes in the human genome show some allelic variation, although the extent to which the alleles differ, and their relative frequencies, varies from gene to gene. Much of this allelic variation will be neutral and some will be deleterious mutations that have not yet been removed from the gene pool, but some of it may represent adaptive mutations that have not yet reached fixation. Geneticists can detect alleles that are under positive selection since such alleles increase in frequency more quickly than recombination can randomize their associations with adjacent genetic sequences. This generates a characteristic pattern of linkage disequilibrium between selected alleles and surrounding DNA (see section 2.3.1).

Researchers have found the hallmarks of current positive selection for around 7% of human genes (Voight *et al.* 2006; Wang *et al.* 2006). This means that for each of these genes (as many as 2,000 in number) there is an allele which is not yet at fixation but which is rapidly increasing in frequency in at least part of the human population. Hawks *et al.* (2007) tested the population frequency distribution of these alleles against the assumption that adaptive evolution had gone on at a constant rate throughout human history. This assumption was rejected. Instead, it looks like the rate of selection has greatly accelerated in the last 40,000 years.

Why would this be? One reason is that the human population has grown much bigger in the last few thousand years and larger populations generate more variation to be selected. The second reason is that, in the last 40,000 years, and particularly the last 10,000 years, humans have been constantly colonizing new niches; first, the areas outside the tropics, then the agricultural and herding niches rather than those of hunter-gatherers. These transitions would have changed the adaptive landscape and provided new problems to solve, so we might expect them to lead to a flurry of evolutionary change. For example, many of our currently most deadly infectious diseases only became a problem for humans once we began to live in denser groups and in close proximity to domesticated animals, events that have only occurred in the last few thousand years. This creates a whole new set of selection pressures, and genes involved in immunity are particularly likely to show evidence of current selection (Wang *et al.* 2006).

Ongoing selection at the phenotypic level

Biologists often do not know which, if any, genes contribute to variation in a trait, but they can nonetheless look for evidence of selection at the phenotypic level by testing whether there are non-random associations between a phenotypic characteristic and some component of reproductive success. When this is done for humans, it is easy to find evidence of stabilizing selection. For example, babies of around average birthweight have fewer health problems than those that are extremely large or extremely small. However, again, stabilizing selection only maintains the status quo. Is there any evidence of directional selection at the phenotypic level?

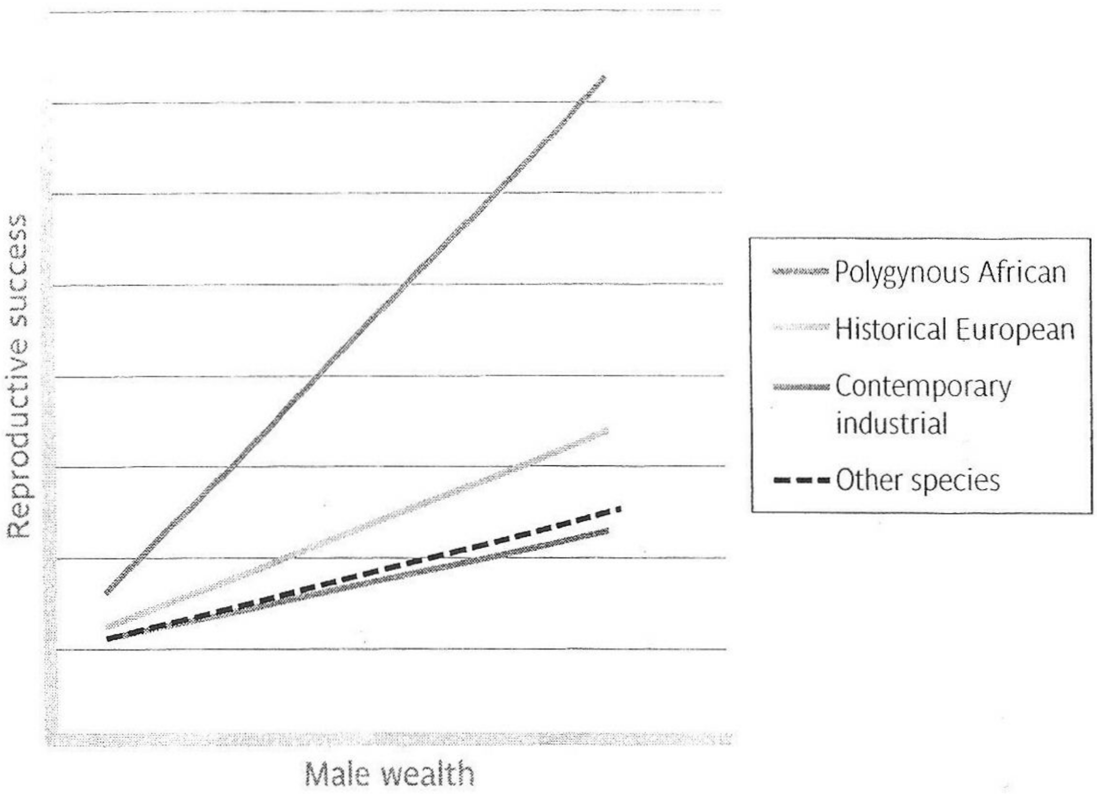
Nettle & Pollet (2008) reviewed the evidence for positive selection on male wealth across eight contemporary and recent human societies. It seems to be something of a cross-cultural universal that in societies with accumulatable wealth, richer men have higher reproductive success, and indeed we found positive relationships in rural African, historical European agrarian, and contemporary industrial societies. The strengths of the relationships were different in the different types of society (Figure 11.1) and the relationships also came about in rather different ways. In the rural African societies, rich men had more wives, and hence many more children, and the slope of the relationship was very steep. In contemporary industrial societies, there was no polygyny and family sizes were about the same for all social classes, but rich men were much less likely to remain childless than poorer men were. Even the weaker relationship found in the contemporary industrial societies was as strong as many selective gradients reported by field biologists working on other species.

Thus, natural selection on male wealth is still going on, even in contemporary Britain and the USA. We do not know if this selection is leading to a change in gene frequencies, because we do not know if the attributes that make men likely to become wealthy exhibit heritable variation, but if there are alleles in any way, however indirectly, associated with greater likelihood of accruing wealth, then they will be increasing in frequency.

11.1.3 From genotype to phenotypic consequence: DRD4 in the Ariaal of Kenya

A rare study of ongoing selection that included both genotypic and phenotypic information is Eisenberg *et al.* (2008). The study concerns a polymorphism of a gene called *DRD4*, which codes for the receptor of a brain neurotransmitter called dopamine. Dopamine is involved in the control of reward-driven behaviours such as eating and the approach to novel situations. This gene is highly polymorphic in the human population. There are two main groups of alleles, those with seven repeats of a particular 48 base pair sequence, and those with a different number of repeats, most commonly four. An individual with at least one copy of the seven-repeat allele is said to have a 7R+ genotype, and an individual with no such copy, a 7R− genotype.

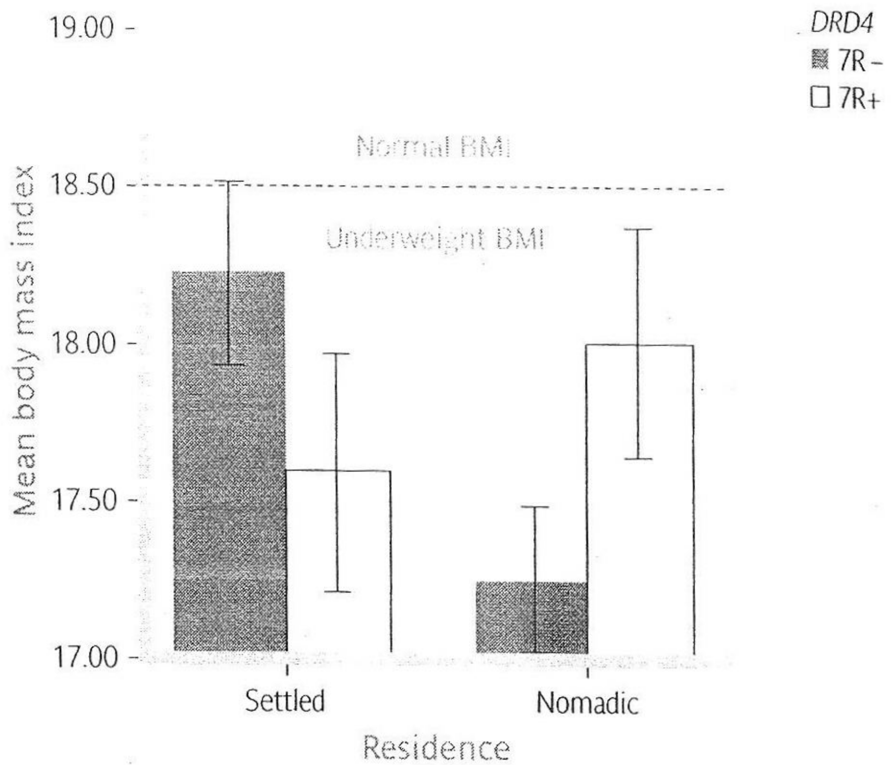
Figure 11.1 Relationships between male wealth and reproductive success across three types of human society: African polygynous, historical European agrarian, and contemporary industrial. The dotted line shows the median selection gradient from a large database of studies of ongoing selection on various characteristics in species other than humans. *After Nettle & Pollet (2008).*



It had previously been noted that 7R+ genotypes are more common in populations that are nomadic or have a recent history of migration. Thus, it is possible that something about the reward-seeking behaviour of 7R+ individuals increases fitness when the population have to move around to find resources, but not when it is settled. A unique opportunity to test this hypothesis came from the Ariaal of Kenya. This is an ethnic group that traditionally practised nomadic livestock herding. Part of the group has been settled for about 35 years and has begun some agriculture, whilst the remainder continues to be nomadic. This is a very impoverished part of the world and both parts of the population are under nutritional stress.

The frequencies of the 7R+ genotypes were the same in the settled and nomadic populations, which is not surprising since they only have a generation or two's separation. However, in the settled population, individuals with the 7R+ genotype were considerably more underweight than those with 7R–, whilst in the nomadic population exactly the reverse was true (Figure 11.2). Given that body mass in this population is going to be a major determinant of survival and reproductive success, this suggests that 7R– is under positive selection in the settled group and 7R+ is under positive selection in the nomads. This concurs with the frequency distribution of the two alleles across populations.

Figure 11.2 Body mass index (BMI) of settled and nomadic Ariaal men by *DRD4* genotype. The 7R– allele appears to provide an advantage in getting resources in the settled context and the 7R+ an advantage in the nomadic one. Note that this is a nutritionally stressed population and so all BMIs are in the underweight range. Error bars represent one standard error. *From Eisenberg et al. (2008).*



11.2 Evolution leaves a legacy

The previous section has shown unambiguously that evolution is still going on in human populations. However, natural selection on a trait does not have to be still operative for evolutionary explanation to be relevant to that trait. Consider animals in zoos. The selective pressures on these animals have been to a considerable extent relaxed by the provision of abundant food, the removal of predation, and the treatment of disease. However, zoo animals still behave in the ways that they are adapted to behave. The nocturnal animals are still active in the dark, even though there is now no selective advantage for them in doing this. The large carnivores are still motivated to cover a large range, even though they have no actual need to hunt. The herbivores are still vigilant when out of cover, even though there is now no predation. Thus, to a considerable extent, behaviour reflects the environment of evolutionary adaptedness and not necessarily the current one.

This principle has a number of applications to contemporary human behaviour. For example, New *et al.* (2007) showed that when viewing complex scenes, young Americans spontaneously allocate more attention to animals than to other types of object. This is true even when the other objects are matched for visual properties and mobility. What is interesting about this is that these participants would not encounter animals particularly often, and animals would not much affect their reproductive success either way. They would do better to allocate attention to automobiles, which are the major threat to their survival in the environments that they actually live in, but they allocated rather little attention to automobiles compared with elephants.

This makes sense if we consider that the psychological mechanisms that control attention bear the legacy of thousands of years of evolution in which keeping track of animals—either to eat them or to avoid being eaten by them—was essential to reproductive success and automobiles played no part. These people now live in an environment where fitness depends on the ability to deal with automobiles, but the evolved psychological mechanisms may not be particularly well prepared for the task. Similarly, people tend to fear things like snakes, spiders, and open spaces with no cover. This may have made some sense in ancestral environments, but makes much less in an environment where snakes and spiders pose no danger at all and the real dangers are from such things as electric shocks and road accidents.

Arguments based on the idea that we are adapted to past environments but not the current one are called **mismatch hypotheses**. We have already met some others earlier in this book. For example, the ability of women to alter the sex ratio in favour of girls at times when they were short on calories may have been adaptive across a range of ancestral environments. In contemporary Britain, however, the main consequence of the existence of such a mechanism is to make dieting women have more daughters, which provides no actual selective advantage (section 7.2.2). Mismatch arguments are appealing and often plausible, but we return to the topic with some cautionary words about them in section 11.5. Nonetheless, the general point that contemporary behaviour cannot be understood without some appreciation of evolutionary history is a valid one.

11.3 The place of evolutionary theory in the explanation of current behaviour

In this section, we consider how evolutionary theory contributes to providing explanations for current human behaviour. Throughout this book, we have stressed how behaviour can be usefully understood using the adaptationist framework, that is using the idea that behaviours tend to persist because they are adaptive to generate hypotheses about why organisms behave the way they do. However, many of the explanatory frameworks you will have encountered in the human sciences make no overt reference to adaptive fitness or evolution at all. In psychology, behaviour is explained with reference to particular cognitive or brain mechanisms, in anthropology, with reference to particular cultural traditions, and in sociology, to social and political context. None of these explanations usually mentions evolution. What is the relationship between these very different kinds of explanation and the evolutionary ones we have considered in this book?

The answer is definitely *not* that evolutionary explanations are mutually exclusive alternatives to these other more traditional approaches. Unfortunately, you will read many people holding up false choices like 'Is men's greater aggression due to evolution or due to social factors?' The answer is not one or the other, or even a bit of both. Rather, 'evolution' and 'social factors' are not alternatives to each other any more than 'learned' is the opposite of 'evolved' (section 9.1). Evolution is a general framework for understanding living things and 'social factors' is a class of proximate mechanism. To avoid these kinds of conceptual confusions, we need a framework for categorizing different types of explanation and appreciating how to fit them together.

Tinbergen's four questions

Conceptual confusion of the kind exemplified by the question 'Is aggression the result of society, of the brain, or of evolution?' arises all too frequently in behavioural science. The reason for this was understood nearly 50 years ago by Niko Tinbergen (1963). Tinbergen pointed out that when we ask *why* an animal performs a particular behaviour, we can actually mean a number of different things. In fact, there are four major types of question we could be asking, which are the following:

1. *Proximate causation* or *proximate mechanism*: What are the events preceding the behaviour that contribute to its occurrence? These events could be external causes, such as a particular state of the environment which triggers the behaviour, or internal causes, such as particular hormones or parts of the brain that are involved.
2. *Ultimate causation* or *function*: What are the effects of performing the behaviour on reproductive success and, thus, why has natural selection retained the ability to perform that behaviour?
3. *Ontogeny* or *developmental course*: How does this behaviour develop over the course of the individual's life?
4. *Phylogeny* or *evolutionary history*: When in the history of that species did the capacity to produce this behaviour evolve?

Tinbergen's point is that each of these is a valid and important question, and each has its own answer, which can be worked on somewhat independently of the answers to the other three. More specifically, you can never correctly answer question (2) with an answer to question (1), or vice versa. Nor is it a question of having to choose one of the four answers over the others. We ultimately need answers to all four questions and also to appreciate how the four fit together. However, in the immediate term, we just need to be clear which one it is we are answering and not get into fruitless debates where answers to different questions are set against each other as if they were alternatives.

11.3.2 An example: human infant crying

Zeifman (2001) provided a recent example of Tinbergen's four questions in action by considering the phenomenon of the crying of human infants. There are many reasons that infants cry: because of neural activity in a part of their brain called the limbic system, because they are alone, in order to signal to their mothers they need care, because the young of other mammalian species cry, and so on. These explanations are all so different from each other that it is hard to assess their relative merit. Zeifman shows that the four-question framework can be used to organize these different parts of the story into a coherent whole. A summary of some key points is shown in Table 11.1.

Table 11.1 Why do human infants cry? *Adapted from Zeifman (2001).*

Question	Answer	Evidence
Proximate mechanism	*External*: Physical separation from caregiver; cold; lack of food *Internal*: Limbic system; endogenous opioids involved in crying cessation	Observational and experimental evidence Experimental evidence from animal models Effects of milk and sweet-tasting substances Behaviour of babies born to methadone-addicted mothers
Ultimate function	To elicit care and defence from mothers	Triggers of crying Less crying in cultures where infants are carried more Women of reproductive age respond to infant cries Crying found in infant-carrying species when infant is put down and in infant caching species only when mother is at nest
Ontogeny	Peaks at 6 weeks, declines to 4 months, then stable until 12 months After 12 months may be more strategically directed to extort care and not so associated with separation from caregiver	Observational and experimental evidence
Phylogeny	Crying in response to being put down found in all non-human primates (for whom the ancestral state is for the infant to be carried)	Comparative evidence

The answers to the four questions do interweave in various ways. The fact that the main proximate cause of crying in young infants is physical separation from the caregiver and that non-human primates generally carry rather than cache their young are relevant to understanding crying's ultimate function, and successfully predicts that there will be less crying in cultures where babies are carried more often, a prediction that turns out to be true. The fact that there is a shift during ontogeny from crying mainly when *not* with the caregiver to crying in the company of the caregiver to obtain a resource suggests that crying has different functions at different ages. Thus, investigating one of the four questions helps suggest possible answers to the others, but all four need to be investigated, often using different types of evidence.

To take an evolutionary approach to behaviour is to include question number (2), the question of ultimate function, in one's enquiry. This does not imply that question (2) is the only important one. The others are important too. Nor is it to claim that the behaviour is either 'innate' or 'genetically determined'. Learned behaviours are just as subject to evolutionary analysis as unlearned ones (see Chapter 9). Crying in humans is clearly subject to learning and variation from culture to culture, but as Zeifman shows, this does not prevent a broad evolutionary framework being applied.

Evolution in relation to the human sciences

The crying example allows us to be more precise about how evolutionary explanations fit in with the explanations offered by the traditional human sciences. Research in these disciplines has generally been concerned with different aspects of proximate mechanism (or more rarely, ontogeny). For example, a sociologist of crying might research why babies from families in some social classes cry more than those from others (external proximate mechanism). An anthropologist might research why babies cry more in some cultures than others (again, external proximate mechanism). A psychologist might study how neural activity in a particular part of the brain initiates crying (internal proximate mechanism), whereas a developmental psychologist might look at the time course of crying's development (ontogeny). All of these research activities are valid and none of them precludes *also* asking the questions of ultimate function and of phylogeny.

Indeed, it is not just that evolutionary enquiries are compatible with investigations of proximate mechanism. They may actually help because if we understand *why* natural selection has produced a particular behaviour or capacity, it might help us search in the right place for the internal and external proximate mechanisms. This dialogue goes the other way, too; understanding the proximate mechanism and ontogeny of a behaviour will often provide key evidence for developing functional hypotheses.

Thus, researchers in all of the human sciences can often benefit from an appreciation of the evolutionary function and history of the behaviours or capacities that they are investigating. This is not an alternative to the mechanistic understandings that they have already developed, but a way of making sense of why those mechanisms are as they are and hopefully of making novel predictions.

In the final sections of this book we will briefly consider two of the most challenging and open evolutionary questions concerning contemporary humans: how is cross-cultural variation best to be explained and how much of human behaviour is adaptive?

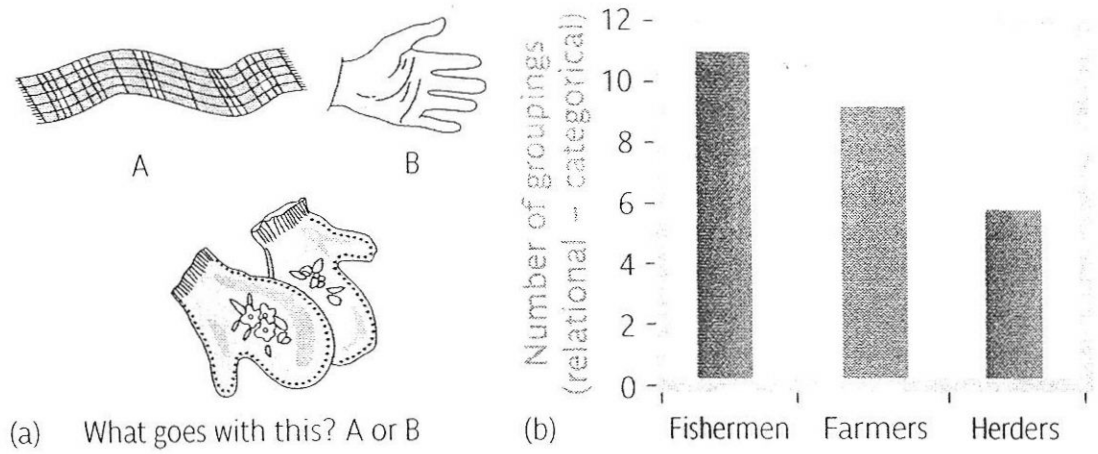
11.4 How should cross-cultural variation be explained?

A striking feature of contemporary humans is their diversity. Some humans are monogamous, some polygynous; some cultures punish women severely for premarital sex, and others regard it as entirely normal. The amount people allocate to strangers in cooperation experiments varies from place to place.

The psychological differences between populations may go deeper than we once thought. For example, Uskul *et al.* (2008) studied groups of fishermen, farmers, and livestock herders from Turkey's Black Sea coast. Previous cross-cultural research has suggested that farmers tend to collaborate and consult with each other, and have a socially interdependent outlook, whilst herders rely more on autonomous individual decision making. This makes sense, given that agricultural activities involve working together with permanent neighbours on joint projects such as irrigation and land management, whereas a herder has his own mobile capital, his herd, which he can decide to take anywhere.

Uskul *et al.* gave their participants a number of cognitive tasks. One example is shown in Figure 11.3. The participant has to choose whether the bottom object goes with A or with B.

Figure 11.3 Livestock herders from Turkey categorize things on the basis of object properties more than relationships, relative to farmers and fishermen from the same region. *From Uskul et al. (2008).*



Either response is possible. To link the gloves with the hand is to emphasize a relationship: the glove and hand work together. To link the gloves with the scarf is to emphasize a type of object: both are winter wear. The fishermen and farmers were particularly likely to categorize on the basis of relationships, whilst the herders were relatively more likely to categorize on the basis of object type (Figure 11.3).

What this suggests is the development of a mindset based on individual objects and their properties in the herders, and based on relationships in the fishermen and farmers. This could well be adaptive given the different life problems that these three groups need to solve, and so the results are not difficult to interpret from the point of view of ultimate function. However, what the proximate mechanism is for the difference is less clear.

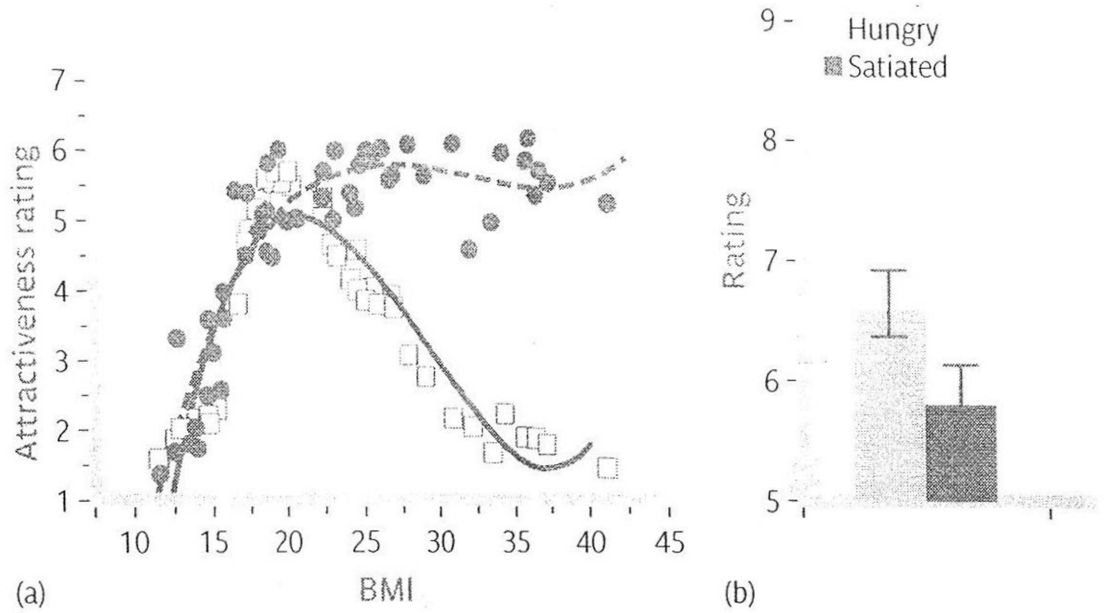
We can eliminate genetic differences between the groups immediately, as the participants all came from the same ethnic and linguistic groups, differing only in their subsistence activity. Thus, some kind of phenotypic plasticity is involved, but how exactly does it work? Evolutionists have considered two main classes of phenotypic plasticity that may underlie cross-cultural differences, known as evoked culture and transmitted culture. We now review them both.

11.4.1 Evoked culture

The idea of evoked culture is that natural selection has produced animals able to exhibit the best phenotype for the environment they find themselves in, across several different environments. They do this by having a range of phenotypes they can produce and a set of cues, either early in development, or in their current context, to which they respond by changing their state. For such a system to evolve, all of the different environmental conditions must have been experienced recurrently over evolutionary time and a number of other conditions must also be met (see section 9.1).

Evoked culture has been compared to a jukebox, where a particular environmental cue presses a button and the appropriate song comes out. There are some good examples of evoked culture in operation in humans. For example, it is well known that men in rural subsistence cultures are attracted to female bodies with more body fat than men from developed urban

Figure 11.4 (a) British men (open squares) prefer female bodies with a BMI (body mass index) of under 20 and find much larger bodies unattractive, whereas South African Zulus (filled circles) find BMIs of up to 40 attractive. *From Tovée et al. (2006).* (b) Hungry Americans express a preference for a larger body size in a mate than satiated Americans (rating here refers to a rating of how large an ideal mate would be). Error bars represent one standard error. *From Nelson & Morrison (2005).*



settings (Tovée *et al.* 2006; Figure 11.4a). This makes adaptive sense; in the rural subsistence context, undernutrition is a real constraint on fertility and an optimal mate would be one displaying sufficient reserves. In the developed setting by contrast, obesity is more likely to be an issue, and a mate signalling dietary restraint is likely to be a healthier one.

The cross-cultural difference in preference could well be evoked culture, but what are the relevant cues? Nelson & Morrison (2005) performed the remarkably simple experiment of assessing American men's preferences for female body size either when they were hungry or when they had just eaten. The hungry men's preferences were shifted a small but significant amount towards larger body sizes (Figure 11.4b).

Thus, it looks as if hunger serves as a cue to evoke preference for fatter mates. Of course, the function of this mechanism is not to make individuals change their preferences between meals. That is just a small side-effect. Rather, where hunger is widespread or chronic, mate preferences will be shifted enduringly towards larger bodies.

Evoked culture differences have some particular properties, to be contrasted with transmitted culture, which we will meet in the next section. They will appear very fast when the triggering cues appear and will only endure as long as the triggering cues persist, that is you could make Western men like rural African men simply by making them hungry and make rural African men more like Western men just by making food more abundant. The exception is where the system relies on developmental induction by early life cues, in which case there will be a time lag of a generation or so for behaviour to respond if the environment changes radically. Evoked culture, however, does not rely on generations of accumulated cultural history or on social learning. It is a more immediate individual response to the current situation. When South African men move to the UK, for example, their body preferences soon converge on the UK norm. For this reason, some people prefer not to refer to evoked culture as 'culture' at all, since although it leads to cross-cultural differences in behaviour, it does not involve persistent socially learned traditions.

Transmitted culture

Transmitted culture refers to inter-population differences that are the result of generations of social learning, with each generation learning from and modifying the norms of the previous one, who in turn learned from the previous one, and so on. Transmitted culture is a key part of the human ability to adapt to multiple different environments. As we saw in section 9.5.3, social learning in humans leads to cumulative cultural evolution, which produces better and better solutions to problems in the local environment.

Transmitted culture has rather different properties to evoked culture. It can lead to the preservation of apparently arbitrary norms. For example, the fact that Muslims do not eat pork, whereas Hindus do not eat beef, cannot be evoked culture, since there are places in India where there are both Hindus and Muslims experiencing the same environment and yet maintaining different phenotypes. Instead, history matters for transmitted culture. Muslims do not eat pork because they learned this norm from earlier generations of Muslims, who in turn learned it from still earlier ones. This does not mean that it is not adaptive, but it means that it might not be; it could be something that got fixed by benefit or by chance many centuries ago and now persists neutrally or even maladaptively (see section 11.5).

Where cultural differences are transmitted rather than evoked, we expect to see a rather different pattern. There may often be a long lag when the environment changes but the culture stays the same, since people are depending on what previous generations did rather than on input within their own lifetime. Also, the environment that a population came from will often predict their behaviour better than the one they are currently in. Finally, cultural traditions that are transmitted will themselves exhibit a kind of evolution. They will develop, mutate, split, and change in complexity over time, as each generation learns something that is slightly different from what the previous generation did.

It is hard to say whether the cognitive differences between farmers and herders described by Uskul *et al.* (2008) are best viewed as evoked or transmitted culture. It is plausible that performing cooperative tasks would evoke an appropriate mode of cognition. On the other hand, there is some evidence for cultural lag, with regions of the world such as the southern states of the USA, which were once peopled by herders, retaining individualistic social norms for many generations after the herding itself has ceased to be the mainstay of the economy (Cohen & Nisbett 1996). This suggests a role for social learning and transmitted culture.

11.5 How much of our behaviour is adaptive?

In this section, we consider the issue of how much of our contemporary behaviour is adaptive, that is to what extent do the decisions that contemporary humans make about what work to do, when to marry, how many children to have, and who to name in their wills actually maximize their reproductive success?

The answer we give to this question will depend on what kinds of proximate mechanisms for decision making we believe that humans have evolved. There is a diversity of opinion amongst evolutionary scientists on this question. In fact, there are three major current styles of evolutionary approach and the central differences between them concern the extent to which current behaviour is adaptive. They are generally known as **evolutionary psychology**, **human behavioural ecology**, and **gene-culture coevolution theory**. In the next three sections, we review each one briefly and illustrate the differences between them by considering how each one might approach the excessive consumption of fats and sugars that is common in the contemporary developed world.

11.[illegible] Evolutionary psychology: behaviour adaptive for the ancestral environment

The evolutionary psychology approach has been developed largely by psychologists concerned with understanding why particular brain and cognitive mechanisms work in the way that they do. The hypotheses it creates are adaptationist ones, but the adaptation in question is not so much to the current environment as to the ancestral environments in which the human brain evolved. The ancestral environment is not, of course, any particular time or place. It is a statistical composite of all the contexts in which human ancestors have lived, weighted towards the most recent. However, since the period humans spent as hunter-gatherers so dwarfs the period since the transition to agriculture (see section 10.2.4), the environment of evolutionary adaptedness is often conceptualized as a kind of archetypal hunter-gatherer society.

Evolutionary psychology does not, contrary to accusations sometimes levelled at it, assume that human behaviour will be the same in all contexts. It allows for phenotypic plasticity. However, the plasticity it allows for is mainly of the evoked culture kind (see 11.4.1) and adaptive plasticity of this kind can only evolve if all of the different environmental states have been experienced recurrently over evolutionary time. Thus, humans can be expected to behave in ways that would have been adaptive in ancestral environments and will only behave adaptively for the contemporary environment to the extent that this resembles an ancestral one. In other words, evolutionary psychology makes heavy use of mismatch arguments.

Let us see how an evolutionary psychology approach might apply to the contemporary problem of obesity in the developed world. Much of this obesity is proximately caused by people eating more sugar and fat than is good for them. In ancestral environments, sugars (in the form of fruit and honey) and fats (animal products) were rather scarce, transient resources, and so it made sense to be motivated to fill up on them whenever they were available. This caused no health problems as the supply was never sufficient for people to overeat on them. It causes health problems now because the unprecedented abundance of synthetic fats and sugars is not something our evolved appetites have equipped us to handle. As Nesse & Williams (1995: 148) put it:

> Our dietary problems arise from a mismatch between the tastes evolved for Stone Age conditions and their likely effects today . . . Fat, sugar and salt were in short supply through nearly all of our evolutionary history. Almost everyone, most of the time, would have been better off with more of these substances, and it was consistently adaptive to want more and to try to get it.

This argument certainly has some face validity, given the high intrinsic palatability of sweet and fatty foods to humans.

Evolutionary psychology is a thriving discipline. Its central premises are valid and it is true that there can be mismatches between current and ancestral environments. However, some caution and sophistication are required concerning how evolutionary psychological theories, and in particular mismatch arguments, are deployed. The reasons for this are the following:

1. Time: Evolution can happen a lot more quickly than was once thought. Even a modest selection gradient (like the dotted line in Figure 11.1), when coupled with reasonable heritability, can generate one standard deviation's change in a phenotypic characteristic in around 25 generations. This is still 500 years, but it is a lot less time than the time lag since the Pleistocene. Thus, it is perfectly plausible that there has been significant adaptation to agrarian and even city life.
2. Variety of past environments: The term 'hunter-gatherers' actually lumps together some very different ways of making a living. Human hunter-gatherers varied enormously in the types of ecological problems that they confronted. They ranged from almost complete to rather little dependence on large game animals, from large groups to small, from highly mobile to more concentrated around aquatic resources, from deserts to lakes. For at least 40,000 years, the hunter-gatherers who formed our ancestors were to be found anywhere from the equator to the temperate latitudes, experiencing enormous changes in ecology as the glacial periods gave way to interglacials. Thus, at the very least, we would expect evolution to have a high degree of evolved plasticity in humans for coping with different types of environment. This is not a problem for all mismatch arguments. Certain features (such as scarcity of sugar) may have been recurrent across all these ancestral environments, but different in the contemporary one, and these would be the features most likely to lead to maladaptive behaviour in the present. However, it is a problem for any attempt to explain current human tendencies as evolved for any very specific ancestral ecology.
3. Diversity of human social organization: The diversity of human social organization, as documented by anthropologists, is impressive. There are matrilineal and patrilineal societies, societies with marriage for life and societies where relationships come and go, polygynous and polyandrous societies, and so on. Again, this is not contrary to evolutionary psychological explanations per se, since they allow for extensive phenotypic plasticity via such mechanisms as evoked culture. However, some early evolutionary psychology underemphasized cross-cultural variation and perhaps the most exciting current areas of research concern how evolved plastic mechanisms lead to the observed cross-cultural variation in behaviour (e.g. Gangestad *et al.* 2006).
4. Nature of human adaptations: As discussed in section 10.3.5, humans display a suite of characteristics suggesting that they are highly adapted for the learning niche: large brains, extended juvenile period, slow life history, and long life. This adaptive package allowed humans to colonize a variety of different habitats by acquiring locally relevant adaptive knowledge during their lifetimes. This suggests we should expect a sophisticated ability to find new ways of behaving adaptively when the environment changes.
5. Nature of the current environment: Finally, it is easy to assert that the contemporary urban environment is so different from the environments of our ancestors that we are not adapted to making good decisions in it, but less easy to show in exactly which respects it lies outwith the range of ancestral environments. In all environments, humans have

> to figure out a good way of getting resources, learn to eat the right stuff, master the local technology, retain social allies, avoid disease, attract a mate, trade-off energy spent in reproduction against the accumulation of resources and the maintenance of alliances, and trade-off investment in a current relationship against a future one, investment in children against investment in grandchildren, and so on. Modern urban environments embody these timeless dilemmas just as earlier ones did, and although the solutions might be different, the problems are the same to a surprising extent.

These problems all counsel against over-using (or using too simplistically) the idea that we are 'Stone Age' minds living in modern societies, although they are certainly not arguments against invoking ultimate function and evolutionary history in trying to understand human cognitive and neural mechanisms.

Human behavioural ecology: behaviour adaptive for the current environment

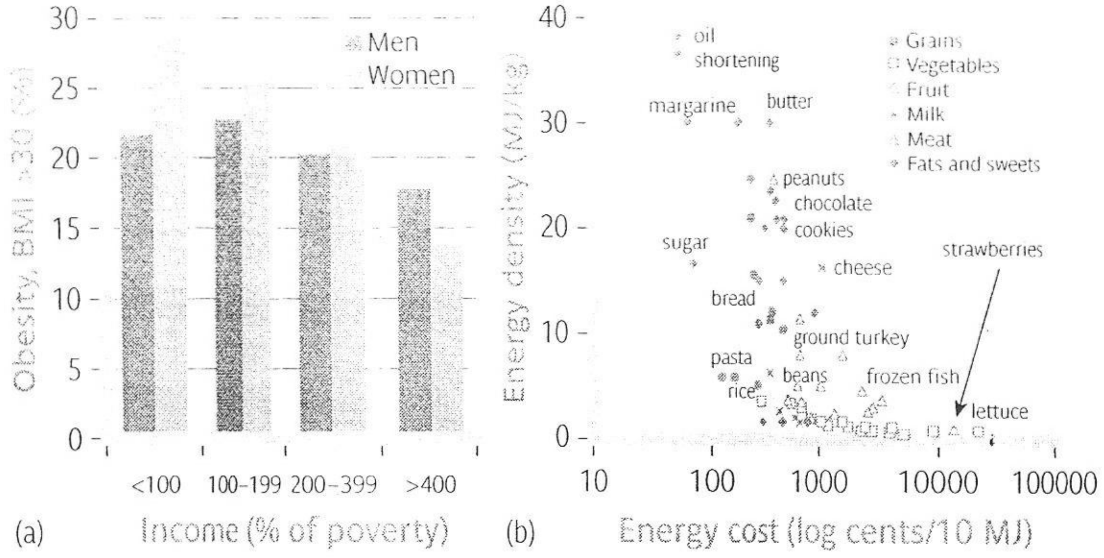
The second major evolutionary approach to modern humans is known as human behavioural ecology. Human behavioural ecology comes out of anthropology, and uses many tools developed for the study of animal behaviour. Its main focus has been on how the behaviour seen in various non-Western, usually subsistence, societies can be understood as an adaptive response to the local ecological conditions. Thus, human behavioural ecology has been quite successful at explaining why some societies are matrilineal and some patrilineal, or why some are monogamous and some polygynous, and many other traits.

Human behavioural ecology is also an adaptationist approach, but it is the current environment, not the ancestral one, for which behaviour is seen as adaptive. Thus, a large part of the research effort of human behavioural ecology is directed at the careful measurement of the current environment, and the assessment of what behavioural options are available to people in it and what their payoffs might be. The behaviours that maximize reproductive success are then predicted using some kind of optimality model. The attention to current context is a feature that human behavioural ecology shares with ecology more generally, but also with the more traditional social sciences. Central to anthropology and sociology, for example, is the idea that current context shapes behaviour, and thus that current context must be deeply understood. Human behavioural ecology makes little use of the ideas of the environment of evolutionary adaptedness or of mismatch.

Human behavioural ecology assumes that humans have considerable phenotypic flexibility, presumably through having evolved a general motivation to maximize reproductive success, and extensive abilities to learn and to experiment in pursuit of this goal. However, human behavioural ecologists have not really been concerned with what the psychological processes leading to behavioural flexibility are. They are really interested in answering the question of ultimate function of behaviour (see section 11.3.1) and are agnostic about the proximate mechanisms.

How might a human behavioural ecologist approach the issue of modern overconsumption of sugars and fats? The first thing that careful research would reveal is that it is not *everyone* in the contemporary USA who shows this behaviour. It is socially patterned, with poor diet and obesity being much more common amongst those on low incomes (Figure 11.5a). The reason this might be the case is further elucidated by considering the relative costs of different foods. Figure 11.5b plots the energy density of different food types (the calories per kilo, as it were)

(a) The proportion of Americans who are obese (body mass index, BMI, >30) as a function of their incomes. Poor women are particularly prone to obesity. (b) The energy density of different food types plotted against their energy cost. Fats and refined sugars supply calories at much lower cost than fruit and vegetables. *From Drewnowski & Specter (2004).*

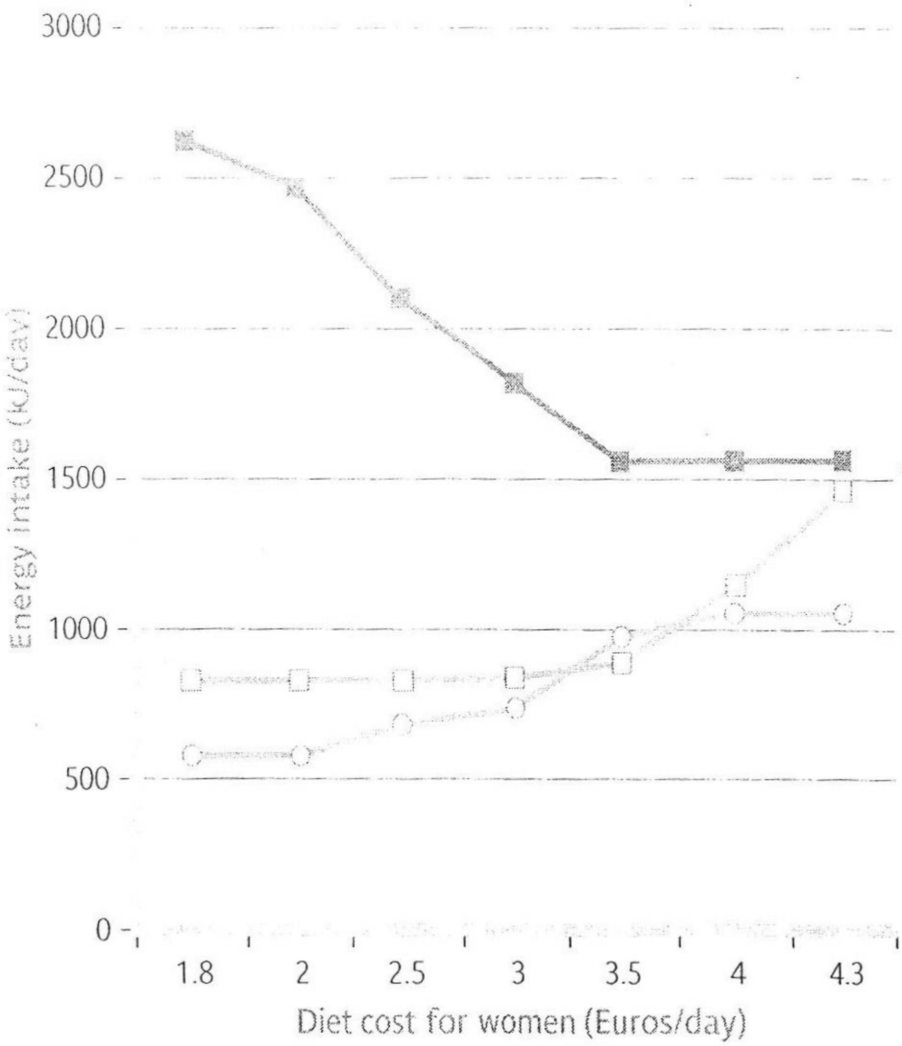


against their current cost in the USA (the dollars per calorie). You can see that fats, sugar, cookies, chocolate, and so on are dense in energy and provide each calorie much more cheaply than do lean meat, fruit, or vegetables (Drewnowski & Specter 2004). Thus, it could be that people with limited dollars to spend actually have no better strategy available to them than getting their calories from the cheapest source. In support of this view, UK women with healthy diets spend around £600 more on food per year than those women with what would be considered poor diets (Cade *et al.* 1999).

Darmon *et al.* (2002) produced a mathematical model, incorporating the actual costs of different foods, in which they predicted diets using the assumptions that (a) the people need to take in a certain number of calories per day, (b) they want as balanced a diet as possible, but (c) they have a fixed amount of money that they are able to spend per day. The predictions of the model (Figure 11.6) are that as the budget gets smaller, greater and greater proportions of the calories have to come from cheap fats and sweets, and less and less from animal products and particularly from expensive fruits and vegetables. This is exactly the behaviour that poor people in Western countries exhibit.

This puts quite a different slant on the obesity problem. Rather than everyone doing something that would have made sense in the ancestral environment but makes no sense now, people may be choosing the best diet that is available given the resources that they have to spend. This means that the high sugar and fat consumption of the poor is, in fact, adaptive. By adaptive here, we do not mean that this diet promotes the best possible health. In the long term, it causes a lot of health problems. Rather, we mean that given a limited budget, this is the only way available to obtain one's daily ration of calories. When the budget available is increased, people obtain the calories in a way that is more healthy in the long run.

Predicted diet composition for women needing to obtain 1748 kcal of energy per day but with different budgets to spend, from the mathematical model of Darmon *et al.* (2002). Filled squares, fats and sweets; open squares, meat, fish, and eggs; open circles, fruit and vegetables. *Reproduced from Drewnowski & Specter (2004).*



11.5.3 Gene-culture co-evolution: adaptive social learning

The third evolutionary approach to contemporary human behaviour comes from the literature on social learning and cultural evolution. This area is sometimes called gene-culture coevolution theory, dual inheritance theory, or just cultural evolution. The idea here is that humans have evolved capacities to use social learning to obtain locally appropriate behaviour. This produces cumulative local cultural traditions which proximately cause the different behaviour of individuals in different populations.

This is also an adaptationist approach, in that it is based on the idea that the ability to learn socially increases fitness. However, although the ability to learn socially might be an adaptation in general, not every behaviour so learned maximizes reproductive success. For example, in the process of acculturation, I might obtain the adaptive belief that a certain plant is poisonous and also the maladaptive or arbitrary belief that this plant has to be danced around whenever it is encountered. Social learning would persist as long as the information so learned was on balance much more useful than harmful, but I could still acquire a lot of useless beliefs in the process. When the environment changes, there can also be a cultural lag of a number of generations before behaviour adaptive for the new situation is learned and spreads.

Gene-culture co-evolution theory makes quite specific predictions about when behaviour will be adaptive for the current environment and when it will not (see section 9.6.2). At equilibrium, there is always a mixture of reliance on social learning and individual checking that what is so learned is actually useful, and the ratio of social to individual learning depends on the cost of individual learning. Where it is relatively easy to learn for oneself what the fitness consequences of alternative behaviours are, culture will change quickly and usually produce the optimal behaviour for the current context. Where learning for oneself is hard, there can be long cultural lags where an outmoded behaviour persists, or even the spread of a behaviour that is not actually good for reproductive success.

How might gene-culture co-evolution theory approach the problem of overconsumption of sugars and fats? One way might be to look at how dietary preferences are actually formed. It is quite plausible that to a considerable extent people learn to eat what their parents ate. This will lead to a local cultural tradition of diet, which may well be optimized for the local environment (in which case there is no tension between a gene-culture co-evolution account and a human behavioural ecological one; the former is merely providing a proximate mechanism for the behaviour predicted by the latter to be generated). However, if, for example, people become more sedentary, the diet may now be too energy rich and obesity may ensue. This is a kind of mismatch argument too, but the time lag is not the time required for genetic evolution to happen, but the time required for cultural change to happen. The maladaptive cultural state will not endure forever. Instead, some innovators will originate a different dietary pattern, obtain a better payoff, and then perhaps be emulated, leading to a spread of their dietary norms through the population. The exact dynamics of the spread may be uneven, and can be modelled if enough is known about who learns from whom and what the social structure of the population is.

11.5.4 Synthesis

The different emphases of the three main evolutionary approaches are summed up in Table 11.2. All are united by an interest in Tinbergen's question of ultimate function, and thus they are all evolutionary approaches. However, they are concerned with proximate mechanisms to different extents and differ very considerably in their predictions about issues such as how quickly humans can respond with adaptive behaviour if their environment changes in some unprecedented way.

Although I have stressed the differences between the approaches in the foregoing discussion, they also have considerable scope for complementarity. Human behavioural ecology concentrates on ultimate function but tends to be agnostic about proximate mechanisms, relying on some general notion of flexibility or learning. However, merely to evoke learning is a non-explanation; there are many types of learning, each produced by different types of evolved decision-making mechanisms with different design features (see Chapter 9). Thus, evolutionary psychology, with its focus on cognitive mechanisms, can enrich human behavioural ecology's explanations with an account of how behavioural flexibility actually works. Gene-culture co-evolution theory also provides one set of mechanisms for locally adaptive behaviours to become established, namely through social learning, and thus can also enrich the ultimate

Key features of the different evolutionary approaches to human behaviour

Approach	Focus	For which environment is behaviour adaptive?	If environment changes in an unprecedented way, how quickly can adaptive behaviour respond?
Evolutionary psychology	Internal proximate mechanisms (e.g. brain circuits) and ultimate function	Environment of evolutionary adaptedness (EEA); contemporary environment only to the extent it resembles the EEA	At the speed of genetic change
Human behavioural ecology	Ultimate function	Current environment	At the speed of individual learning
Gene-culture coevolution	External proximate mechanisms (e.g. social learning dynamics) and ultimate function	Environment in which that cultural tradition developed	At the speed of cultural change

explanations of human behavioural ecology. Social learning is only possible because there are evolved cognitive mechanisms to make us learn from each other, and thus there is room for collaboration between evolutionary psychologists and gene-culture co-evolutionists on what the nature of these mechanisms is.

On the central issue of whether current behaviour is best seen as optimized for the genetically ancestral environment, the current environment, or the culturally ancestral environment, the answer seems to be that it depends. Different problems need careful study on a case-by-case basis. Some really complex questions, such as why the fertility rate has become so extremely low in developed countries, can probably only be answered by invoking a combination of flexible responses to changing conditions, cultural dynamics, and mismatch with the ancestral environment (Borgerhoff Mulder 1998). Thus, all three approaches have a useful contribution to make.

Human evolutionary behavioural science

Many evolutionary researchers, such as myself, try to incorporate elements of all three traditions into our work to give the best explanations possible for particular cases. There is no clear consensus on what this broad evolutionary approach should be called. Evolutionary psychology *sensu lato* (which means 'in the broad sense') has been suggested, as has human evolutionary behavioural science (Sear *et al.* 2007). Perhaps our best hope is that it would not need a separate name or separate subdiscipline at all. Instead, researchers in all the existing human sciences will simply incorporate evolutionary perspectives, and the framework of Tinbergen's four questions, into what they do. Thus, the Darwinian worldview, with all the beauty and explanatory power that it provides, will become as automatic for those studying humans as it already is for those studying all the other organisms on this earth.

Summary

1. Natural selection in the contemporary human population is still going on and has been observed at both the genetic and the phenotypic levels.
2. There are at least four different types of explanation we can give for a behaviour in terms of proximate mechanism, ultimate function, ontogeny, and phylogeny. The existing human sciences have been mainly concerned with proximate mechanism, and evolutionary approaches can enrich these by adding the angle of ultimate function.
3. Cross-cultural differences in humans are abundant and can be explained by evolved mechanisms of evoked and transmitted culture.
4. There are three major styles of evolutionary approach to modern human behaviour: evolutionary psychology, human behavioural ecology, and gene-culture co-evolution theory. They often make different predictions about the degree to which current behaviour is adaptive, but they are also complementary to a considerable extent.

Questions to consider

1. What will happen to the frequencies of the 7R– and 7R+ *DRD4* alleles in the Ariaal population over the coming generations? What about in the human population more generally?
2. People in developed Western societies have very small families (averaging fewer than two children per woman). Speculate on why this might be, from an evolutionary psychology, a human behavioural ecology perspective, and a gene-culture co-evolution theory perspective.
3. Think about some aspect of people's behaviour that you have experienced in your everyday life and that has puzzled you. How does taking an ultimate, evolutionary perspective help you to understand what is happening?

Taking it further

For core texts in evolutionary psychology, see Tooby & Cosmides (1992) and Buss (1995, 2005); in human behavioural ecology, Winterhalder & Smith (2000); in gene-culture co-evolution theory, Henrich & McElreath (2003) and Richerson & Boyd (2004). Discussions of the relative merits of the three approaches to human evolutionary behavioural sciences are to be found in Smith (2000), Barrett *et al*. (2002), and Laland & Brown (2002). An attempt to integrate across them is made by Sear *et al*. (2007). Two scientific societies that serve the human evolutionary behavioural science community are the Human Behavior and Evolution Society (HBES; http://www.hbes.com) and the European Human Behaviour and Evolution Association (EHBEA; http://www.ehbes.com). Both of these hold annual conferences. Journals with a main focus on carrying human evolutionary behavioural science research are *Evolution and Human Behavior*, *Human Nature*, *Evolutionary Anthropology*, *Evolutionary Psychology*, and the *Journal of Evolutionary Psychology*.