

# Perspectives on human health and disease from evolutionary and behavioral ecology

Beverly I. Strassmann and Ruth Mace

## Introduction

Evolutionary theory can inform the study of antibiotic resistance and other processes that lead to changes in allele frequencies over time (see also Chapters 11, 13, 15, 18, 23). It can also inform the study of genetic variation in susceptibility to disease and identify diseases caused by single genes and others reflecting multiple genes and their epistatic interactions (see also Chapters 2, 3, 4, 5, 6). The focus on genetic variation is important, but it should not eclipse what is actually a much larger picture. Human behavioral ecology uses evolutionary theory to understand patterns of behavior that do not map onto modern-day genetic variation.

For example, the amount of paternal investment that males give to their wives' offspring is more likely to be predicted by cultural variation that influences confidence of paternity than by genetic variation among males (Flinn 1981; Holden *et al.* 2003). A given man is expected to balance his paternal effort and his mating effort to achieve a higher reproductive pay-off than would be possible if he uniformly pursued a single strategy, but switching between strategies does not require the turning on or off of any genes. Behavioral geneticists might approach the problem of dads and cads by studying genetic differences in personality or in strength and attractiveness. Human behavioral ecologists, in contrast, usually consider problems that can be framed in terms of reproductive pay-offs to alternative, flexible strategies. Longitudinal field studies and quantitative cultural comparisons

play a major role. The insights of human behavioral ecology help us to understand the role of evolution in shaping patterns of health and disease that reflect behavioral, social, cultural, environmental, and lifestyle differences. As this is a very large sphere of influence, the implications for medicine and public health are profound.

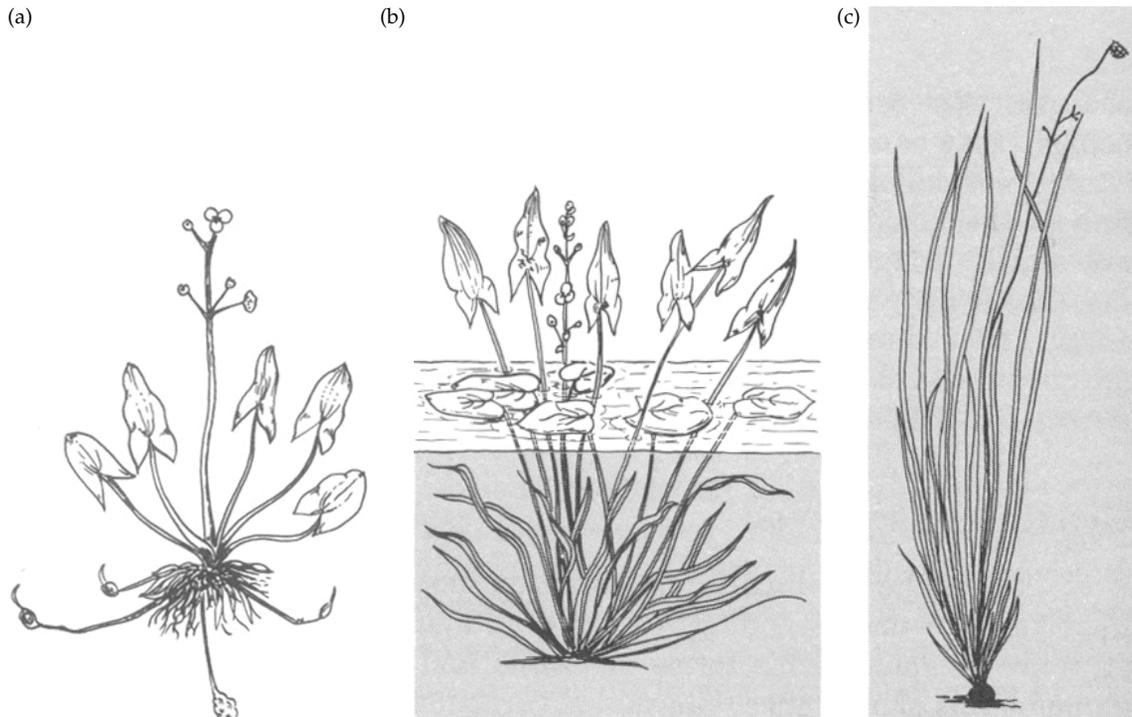
## Phenotypic plasticity

Phenotypic plasticity refers to variation in the phenotype that can be attributed to environmental differences rather than genetic differences (West-Eberhard 2003); this definition does not, however, invoke the false dichotomy of 'nature versus nurture.' Nor does it mean that learning and other phenotypically plastic traits require less genetically transmitted information than do more canalized traits. The same genotype can lead to different phenotypes in different environments, but genes nonetheless play a role in the development of phenotypically plastic traits. Unpredictable and heterogeneous environments select for traits that have a high degree of phenotypic plasticity, whereas stable environments lead to more canalized development. Phenotypic plasticity can be adaptive because it tends to generate a better fit between the organism and the environment. As noted by Alexander (1979: 90), all organisms are to a greater or lesser degree phenotypically variable in ways that enhanced reproduction in the different environments to which they were typically exposed in the past and 'such plasticity is almost the definition of phenotype.'

The arrowleaf plant (*Sagittaria sagittifolia*) is helpful for illustrating the adaptive nature of phenotypic plasticity (Schmalhausen 1949). This plant assumes three radically different forms depending on whether it grows on land or is partially or fully aquatic (Fig. 9.1). The three morphologies result from an interaction between the plant's genotype with its environment during development. The same genotype will lead to different developmental pathways and produce different phenotypes if the environment is altered. A useful concept is the 'reaction norm,' which refers to 'the array of phenotypes that will be developed by the genotype over an array of environments' (West-Eberhard 2003: 101). Since the sensitivity to environmental change is shaped by natural selection, plant species that for many generations have germinated under more homogenous and predictable conditions have diminished plasticity and narrower reaction norms. Thus, rather than being an external property introduced by the

environment, the capacity for phenotypic plasticity is naturally selected and has a genetic basis. We use the example of the arrowleaf plant for its clarity and historical importance, but examples from animals are numerous. West Eberhard (2003) has recently authored a detailed evolutionary synthesis on the developmental processes that generate adaptive phenotypic variation in a wide range of species.

Research on phenotypic plasticity has helped to predict reaction norms for such life-history traits as age and size at maturity (Stearns and Koella 1986; Stearns 1992). A particularly interesting example is the decline in age at menarche by two to five years because of an improvement in nutrition (Stearns and Koella 1986). Poorly fed women mature later, which helps mitigate offspring mortality and increases fecundity by allowing more time for growth, but size at maturity is diminished. Stearns and Koella (1986) model age at menarche as a 'single genotype sliding along a maturation trajectory'



**Figure 9.1** Arrowleaf plant (*Sagittaria sagittifolia*). The three different morphologies illustrate phenotypic plasticity in response to three different environments: terrestrial, semi-aquatic, and aquatic.

Source: Schmalhausen (1949) after Mettler and Greg (1969: 66).

from early maturity at large size attained through fast growth to late maturity at small size attained through slow growth. This example is important in that it links demography to evolutionary biology and shows that reaction norms for age at menarche in humans and age at maturity in other organisms are an evolved response to selection. Stearns and Koella's model partitions the phenotypic response to nutrition, which accounts for a three-year decline in age at menarche, from the genetic change that they predict will eventually (after several thousand years) hasten menarche by up to one year.

In this volume, phenotypic plasticity in humans is illustrated by variations in hormone levels in response to energetic constraints (Chapter 7), the role of the fetal environment as a risk factor for cardiovascular disease (Chapter 19), and the role of diet and lifestyle in the etiology of degenerative disease (Chapter 20). These chapters emphasize physiological and metabolic mechanisms. The molecular mechanisms behind plasticity include genomic imprinting and other epigenetic effects that lead to heritable variation not encoded in the DNA sequence (Chapter 19). Here we focus on plasticity in reproductive and behavioral outcomes and mention the intervening mechanisms only sparingly.

In human behavioral ecology, the term phenotypic plasticity is invoked to explain the role of natural selection in shaping and constraining learned behaviors and many other aspects of an organism's flexible response repertoire. The major organ responsible for phenotypic plasticity in humans is the brain. The unusually large brain of humans is a web of adaptations that allow us to deal with our complex, shifting, and unpredictable social environment (Humphrey 1976; Alexander 1989, 1990; but see Kaplan *et al.* 2000). The complexity of the human social environment reflects ever-changing conflicts and confluences of interest among individuals and groups in human societies (Alexander 1989, 1990). Human intelligence teaches us how to be sophisticated negotiators of our social world, and we use language to manipulate this world in our interest (Alexander 1989; Dunbar 1996). Rather than pitting genes *against* learning, evolutionary ecologists understand that we have genes *for* learning. In a fluid and unpredictable environment, learning confers fitness advantages over fixed and inflexible

strategies. Behavioral ecologists leave to neuroscientists and psychologists the laboratory study of brain mechanisms and instead look at observable patterns of behavior in the real world. They expect that environmental input into the phenotype does not simply create noise, but that it leads instead to context-specific adjustments in behavior that enhance the reproductive success of individuals. A vast body of research demonstrates that even non-human animals, with their much smaller cognitive capacity, make adaptive 'decisions' that are condition-sensitive (West-Eberhard 2003). For example, if you are an echiuroid worm (*Bonellia viridis*), a chemical in the environment during your larval development will direct you to become male or female (Mettler and Greg 1969). Your body evolved to respond to this chemical because it is a reliable cue regarding the fitness pay-offs you can anticipate from your 'choice' of gender.

Reproductive 'decisions' involve the brain, but need not be any more conscious or purposeful than the spinal reflex or the cerebral regulation of the heartbeat rate. At a conscious level, people tend to focus on immediate goals such as attracting a mate, sex, creating families, striving for status or wealth, staying warm and sheltered from the environment, helping their kin, forming alliances and friendships, and pursuing a means of subsistence. These goals tended to translate into enhanced reproduction over the human evolutionary past. When a person pursues these proximate stepping stones, she is engaged in reproductive striving even if she assumes these goals are ends in themselves (Alexander 1979; Irons 1979). In traditional societies that allow polygynous marriage and lack contraception, these stepping stones demonstrably lead to enhanced reproductive success, but in industrial societies, proximate goals may become uncoupled from their ultimate function (Irons 1998). For example, among the Kipsigis of Kenya, the Dogon of Mali, and nineteenth-century Mormons of Utah, wealthy, high status men had more wives and more offspring (Mealey 1985; Borgerhoff Mulder 1987; Strassmann 2003), whereas high-status Canadian men had higher mating success, but did not have more children (Perusse 1993). The critical difference was socially imposed monogamy and contraception in Canada—both recent inventions absent

over most of human evolutionary history. Human behavioral ecologists recognize that adaptation is expected only when genes and the environment are matched to each other and that after rapid environmental (including cultural) change, natural selection will lag behind (Chapter 1).

Four of the theoretical cornerstones of evolutionary theory that might interest physicians and public health workers include: (1) kin selection, (2) life history, (3) parental investment, and (4) sexual selection theory. We present medically informative examples of these theoretical perspectives to suggest how physicians can profitably use behavioral ecology to understand a wide array of medical and public health problems, including child abuse and homicide in step families; deadbeat dads; attachment disorders; failure to thrive; female infanticide; excess male mortality from accidents, suicide, and disease; risky behavior; immunosuppression; reproductive cancer; marital violence; and genital cutting. We do not suggest that there is a gene for child abuse, marital violence, or any of the other phenomena discussed here. However, our genes give us the capacity for phenotypic plasticity, which means that we should expect a tendency for people to respond to their environments in adaptive ways. Hence, in the absence of environmental novelty and other constraints, the flexible, circumstance-dependent behaviors of humans and other organisms are expected to enhance reproductive success.

### Kin selection theory

The genes found in organisms today are not a random selection of the genes of our ancestors. Instead, the genes that have survived to the present have done so because they were unusually good at making copies of themselves (Williams 1966; Dawkins 1976). Genes get copied whether individuals reproduce directly or indirectly. Direct reproduction refers to an individual's own reproductive success, whereas indirect reproduction refers to the help that an individual gives to siblings, cousins, and other kin. These two forms of reproduction combined constitute an individual's inclusive fitness. Evolutionary biologist W. D. Hamilton defined the precise conditions under which an individual can

enhance her genetic representation in future generations by assisting a genetic relative (Hamilton 1964). Hamilton's Rule states that an individual will get a genetic pay-off from helping a relative if  $rB > C$ , where  $r$  is the genetic relatedness between the donor and recipient,  $B$  is the reproductive cost to the donor, and  $C$  is the reproductive benefit to the recipient (see Chapter 1).

Early critics of Hamilton's theory raised a number of objections that have since been dispelled, including the mistaken notion that kin selection must operate at the conscious level (Dawkins 1979; Alexander 1989). Other researchers worked out the mechanisms by which animals as diverse as primates, social insects, and tadpoles discriminate kin from non-kin. It turns out that animals learn who their relatives are from shared associations, for example, being raised in the same burrow, or, in the case of humans, from being actively taught (Alexander 1990). The learning required for kin recognition further illustrates an important point: learned behavior is often adaptive, and this is especially true when it occurs in social contexts that do not depart radically from past human experience (Alexander 1990). Hamilton's rule states that individuals are expected to flexibly adjust their behavior based on the genetic pay-offs from alternative options (see West-Eberhard 2003: 43). It predicts that humans (and other animals) will:

- (a) preferentially help close rather than distant genetic relatives;
- (b) preferentially help individuals of high reproductive value (who can produce lots of offspring in the future); and
- (c) preferentially help those for whom the cost of helping is comparatively low (see Alexander 1979: 156–7; Madsen *et al.* 2007).

In humans, kin selection is a powerful theoretical framework for understanding patterns of parental investment and health vulnerabilities within families.

To understand the medical and public health implications of kin selection, it is helpful to consider the role played by proximate mechanisms. Proximate mechanisms were favored by natural selection because they tended, on average, to bring about adaptive behavior. Whether a particular

mechanism is adaptive or not is context dependent, but mechanisms that tended to promote fitness in past environments were selectively favored. One such mechanism is known as 'discriminative parental solicitude' (Daly and Wilson 1980). Birds that nest in colonies, such as guillemots, have evolved the ability to distinguish their eggs and chicks from those of other parents, whereas birds with dispersed nesting sites lack such abilities (Birkhead 1978). In colonies the potential exists for eggs and chicks of different parents to get mixed up, so egg recognition enables parents to preferentially invest in their own genetic offspring. Humans are a social animal, and like the guillemot, discriminatory parental solicitude is well documented, especially in step-relationships (Daly and Wilson 1988).

### Step-parents

'Cruel step-parent' stories like the Cinderella tale are widespread and reflect a demographic reality: children are at increased risk of abuse and death in the presence of a step-parent. In a Canadian city, preschoolers living with a presumed genetic parent and a step-parent were 40 times more likely to become victims of child abuse than were children living with both genetic parents (Daly and Wilson 1985). In the United States overall in 1976, fatal child abuse was 100 times more likely when a step-parent was present in the household (Daly and Wilson 1988). In modern times, homicide and child abuse are extreme behaviors unlikely to enhance the reproductive success of the perpetrators; hence they are presently maladaptive. The discriminative parental solicitude from which these pathologies arise, however, is a proximate mechanism that was presumably adaptive, on average, in the human evolutionary past (Daly and Wilson 1988).

Step-parents are much more likely to abuse a child than are genetic parents, but the baseline rate of abuse in step families is still very low (322 fatalities per million Canadian preschoolers) (Daly and Wilson 2001). This brings us to another question: Why do many men benevolently parent other men's children? In a study of men in Albuquerque, New Mexico, Anderson *et al.* (1999) and Lancaster and Kaplan (2000) demonstrated that paternal care can be a form of mating effort. Albuquerque

men invested the most in their genetic offspring whose mothers were current mates and the least in step-offspring whose mothers were former mates. Interestingly, they invested about the same in their genetic offspring whose mothers were former mates as they did in their step-offspring through current mates. The authors conclude that men invest in children partly for the benefit of the relationships they have with the children's mothers.

This study has implications for the public health problem of deadbeat dads who withhold the child support they owe. According to Anderson *et al.* (1999), the reluctance of males to pay support arises from their reluctance to 'direct a significant portion of their mating effort budget into nonmating relationships, decreasing their ability to attract or maintain subsequent mates.' Understanding the psychology of deadbeat dads may be a first step toward solving this pervasive public health problem (Anderson *et al.* 1999). When step-families are formed, explicit education and public awareness about the risks and early warning signs could help reduce the prevalence of tragic outcomes.

### Adoption

Adoption may seem to contradict kin selection theory, but it is easy to understand from a behavioral ecological perspective. In traditional societies in Oceania and other places where adoption has been well studied, the adoptive parents are usually the presumptive genetic kin of the adopted child (Silk 1980). In industrial societies, adoptive parents are often aunts and grandmothers who take over when necessity demands it, as in the case of maternal death or drug abuse, or adoptive parents may be childless. The adoption of a child is arguably an altruistic and humanitarian act, yet such acts are far less common among fertile than infertile couples. If fertile couples commonly preferred adoption over raising genetic offspring, then that would indeed be difficult for evolutionary theory to explain. Psychological and emotional mechanisms of parent-infant attachment play a crucial role and enable most adoptions to be successful. In past environments these mechanisms promoted parental investment in genetic offspring, but these same mechanisms can

be redirected toward nongenetic offspring in the novel environments of today. One novel feature of modern environments is the shortening of the reproductive span due to delayed childbearing, which forces many couples to choose between having smaller than desired family sizes or to complete their families through adoption. Over the human evolutionary past, however, the adoption of nonrelatives was probably rare.

The adoption of older children is often less successful than the adoption of infants because the window of attachment is most pronounced in the first year of life (Carlson *et al.* 2003). In developing countries young children who lose their mothers are about five or six times more likely to die by age 5 years than are children whose mothers survive (Mace and Sear 2005). In the Ache of Paraguay, 100% of motherless children were killed by age 1 year (Hill and Hurtado 1996: 437), although recently such a child was adopted by a bereaved mother who was unrelated (K. Hill, personal communication). Over human evolutionary history the generally high death rate of motherless infants would have diminished selection for the ability to postpone attachment until later in childhood. Not many children were left waiting for a substitute caregiver. Unfortunately, this legacy is problematic for the thousands of orphaned children who are institutionalized and who do not find families before they are toddlers or older (Carlson *et al.* 2003). Policy reforms that speed up adoptions would give life-long, emotional benefits for these children. Another possible reason for the brevity of the window of attachment is that, over the human evolutionary past, the adults who nurtured a child during infancy were more likely to be genetic parents and close kin. Children could trust these individuals more than the step-parents and strangers who followed later. The window of attachment is another example of the adaptive nature of learning (see Chapter 1) and shows that adaptations are a product of genes and the environment. The genes that are around today were favored in past environments, but when a novel situation is introduced (orphanages), then adaptation breaks down (see Chapter 1).

## Life-history theory

### Trade-offs

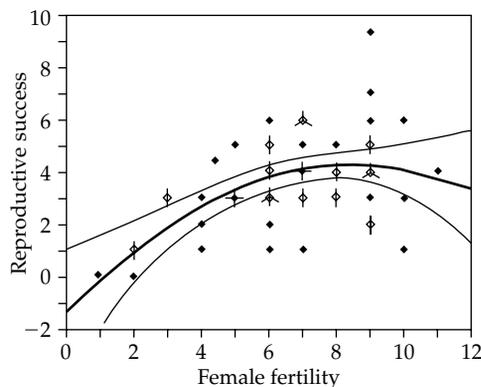
Life-history theory concerns the allocation of resources and time to vital events, ranging from growth and body maintenance to reproduction and death (Stearns 1992). As such it is relevant to most of the chapters in this book. Trade-offs are introduced in Chapter 1 and taken to their inevitable conclusion of senescence and death in Chapters 18, 19, and 23. The essential notion that trade-offs exist is fundamental to understanding human health and development: energy expended on reproduction may not be available for immune function or growth or repair, and the constant repair of a body beyond a certain age may not be the best way for genes to replicate themselves in future generations. Within those resources allocated to reproduction, how much should we devote to mating and how much to parenting? Within those resources allocated to parenting, how much should we devote to producing more offspring versus looking after the children we already have? While medical practitioners operate on the basis of preserving life by whatever means possible, natural selection will balance survival against reproductive gains to maximize not health or survival but inclusive fitness. Thus selection on our physiology and our behavioral tendencies may not always be in the best interest of our own or our children's well being.

Human behavioral ecologists have examined the trade-offs inherent in reproductive decision-making mainly in traditional populations, usually among women who are not using contraception (Cronk *et al.* 2000). These women are experiencing the high energetic and health costs of childbearing in an environment where food is often scarce. It is in these circumstances that we can best understand the selection pressures that operated on our ancestors, some of which may apply even in urban environments today and others of which may not. We review some examples of studies that have helped us to reveal the trade-offs that have shaped human life-history patterns in three different areas: offspring number versus quality, parental effort and longevity, and menopause and the post-reproductive life span.

### Offspring number versus quality

A pioneering study that tested predictions from life-history theory among the Ache found little supporting evidence for these trade-offs, but helped lay the groundwork for studies that came later (Hill and Hurtado 1996). One of these was by Strassmann and Gillespie (2002), who found that Dogon women in Mali, West Africa, experienced diminishing returns to reproductive success (measured as the number of offspring who survived to age 10 years) from higher fertility (measured as the number of live births) (Fig. 9.2). Parents who had many children invested less in each one. For a given child, the odds of death by age 5 years increased 25% for each additional child present in the family (Strassmann 1997). When the ratio of children to married adults in the family increased by one extra child per adult, the odds of death increased nearly threefold (Strassmann 1997). These results held up after statistically controlling for a large number of predictor variables such as wealth; thus they provide evidence for the offspring number–offspring quality trade-off.

Haig mentions in Chapter 6 that closely spaced birth intervals tend to increase infant mortality, yet the strategy of rapid reproductive rate can sometimes favor maternal reproductive success even when it elevates offspring mortality (Hobcraft *et al.*



**Figure 9.2** The relationship between female fertility (number of live births) and lifetime reproductive success (number of offspring who survived to age 10 years) in the Dogon of Mali ( $n = 55$  women,  $R^2 = 0.32$ ). Each 'petal' represents an additional data point. From Strassmann and Gillespie (2002).

1983). This is perhaps most clearly illustrated among mothers of twins. While the overwhelming majority of human births are singletons, twinning occurs in 1–8% of pregnancies (depending on the population). Twinning is an evolutionary puzzle as the health costs and elevated mortality risks to mother and babies are well documented. In rural Gambia prior to the arrival of medical services, twins died within the first month of life at roughly double the rate of singletons—suggesting that twinning has no fitness advantage and thus is maladaptive (Sear *et al.* 2001). Other studies of twinning in pre-industrial Finland found broadly similar results, although if both twins happened to be girls (who are slightly smaller and less energetically costly to bring to term), mortality risks to the mother and her infants were not as great (Lummaa *et al.* 2001). However, in both studies, the mothers who gave birth to twins experienced significantly shorter birth intervals, even if twin births were counted as only one birthing event, and mothers of twins had higher lifetime reproductive success. These findings support the idea that twinning is a by-product of polyovulation (Anderson 1990) and that ovulating from both ovaries each month increases the chances that a cycle achieves a pregnancy. Occasionally a twin pregnancy results, but twins were only carried to term in taller and healthier mothers in the Gambian population. Twin mothers tend to be the supermums of their populations, and on balance, despite their higher infant mortality, they gained enhanced reproductive success from their shorter birth intervals. In the Gambian population, twin mothers are so much more reproductively successful than the non-twinning mothers that twinning appears to be under positive selection pressure. It is tempting to speculate that populations with high twinning rates are those where fast reproductive rates are selected for by high extrinsic adult mortality risks, and one case study suggests this might be the case (Lummaa *et al.* 1998). Another hypothesis is that twinning rates are higher in populations with higher maternal body mass (Bonnelykke 1990).

### Parental effort versus longevity

Twinning illustrates the trade-offs between rapid reproductive rate and mortality risks for babies,

but the increased risk for mothers also needs to be considered. If the central tenet of life-history theory—that energy allocated to reproduction cannot be spent on body maintenance or growth—is true, it could be predicted that high reproductive rate is associated with increased adult female mortality, even after excluding cases of maternal mortality associated with the birth itself. However, in general, no clear association between life span and fertility emerges. Some studies have reported that reproduction shortens the life span in harsh environments (Lycett *et al.* 2000), but these results are controversial (Gavrilova and Gavrilov 2005). Other studies show a positive association between maternal fertility and longevity rather than the predicted negative one (Beeton *et al.* 1900; Gavrilova and Gavrilov 2005), which may reflect phenotypic correlation: fitter individuals experience both higher birth rates and a greater potential for long life. Twin mothers tend to be among the fittest in their populations in terms of phenotype; they tend to be taller, with higher Hb levels (Sear *et al.* 2001). It is not yet clear whether they also live longer than mothers of singletons—but if they do, their higher costs of reproduction are masked by their higher phenotypic quality.

The experiment that needs to be done to demonstrate costs of reproduction, paid through reduced maternal longevity, is to make mothers who would normally have been capable of raising a family of six children raise eight children instead. Do these mothers experience higher mortality? Alternatively, one might make these mothers raise four children and see if they experience increased longevity compared to those left to raise the number of children they naturally bore. Of course the ethics of such an experiment preclude it in humans, but in fact that experiment has been done in birds and some other species. Collared flycatchers and kestrels that had additional offspring introduced into their nests as eggs died younger than if they were allowed to raise the clutch size that they had laid (Daan *et al.* 1990; Gustafsson and Part 1990). In human studies, we can only use sophisticated statistics to try to untangle these phenotypic effects—Doblhammer and Oeppen (2003) do just this and report evidence of a higher cost of reproduction in historical Britain among female aristocrats with

large families. However, their methodology may be problematic in that they dropped from their analysis both childless women and women with only one child (Gavrilova and Gavrilov 2005).

### Menopause and the post-reproductive life span

Both the trade-off between investing in existing or future children and the trade-off between further reproduction and maternal survival combine to explain one of the unique features of the human life history—menopause. While some species have undergone a cessation of reproduction in old age in captivity, humans seem to be the only primate in whom females routinely experience around 20 or more years of post-reproductive life, even in hunter-gatherer societies (Paul 2005). Proximately menopause is caused by atresia—eggs die off rapidly and simply run out by age 50 (with genetically normal eggs running out sooner). Ultimate explanations for why natural selection has designed our physiology in such a way are mostly based on the notion that at some point in later life the costs of continuing to reproduce outweigh the inclusive fitness benefits of helping either offspring or grand-offspring to survive and reproduce (Williams 1957; Peccei 1995; Hawkes *et al.* 1998; Shanley and Kirkwood 2001). The risks of maternal mortality mean that the trade-off between caring for existing offspring or having more offspring comes into play.

Clearly as mothers do not reproduce after menopause in natural circumstances, it is not possible to test empirically what the precise costs and benefits of late reproduction would be, but alternative life histories can be modeled by computer. Shanley and Kirkwood (2001) conclude that human female menopause could evolve if maternal mortality risk is high and increasing with age, and mother and grandmother effects are important in reducing infant mortality and increasing female fertility. While there is some debate in the literature as to whether it was the life span that extended, adding post-reproductive life to a chimp-like fertile span, or whether the termination of reproduction moved earlier in the life course, it is worth noting that models such as Shanley and Kirkwood's treat those two scenarios as functionally equivalent.

In demographic and anthropological studies, one method of assessing the importance of the extended family in the raising of children is to examine the impact the death of each relative has on the chances of survival of a child of each age. Studies of patrilineal, patrilocal populations find that the costs of a mother's death greatly exceed the costs of a father's death, in terms of a child's survival and nutrition, and the survival of a maternal grandmother is associated with more positive child outcomes than the survival of a paternal grandmother (Mace and Sear 2005). The costs of raising a human family with multiple dependent young, unable to achieve self-sufficiency until their teens or later, seems to be a job that benefits from the help of the parents and the extended circle of kin. These studies do not, however, explain menopause as an adaptation because they do not show that the gain in reproductive success from helping children and grandchildren after menopause is greater than the cost to reproductive success from ceasing to maintain fertility. Theoretically, we expect transfers from parents and grandparents down the generations to be enabled by and to select for long life spans, which coevolve with larger brains and delayed onset of reproduction (childhood)—these are characteristics of human life-history strategies that are probably associated with the need to acquire complex skills for survival and reproduction (Kaplan *et al.* 2000; Lee 2003). Further empirical evidence, however, is needed to test this hypothesis and alternative explanations for the unique features of human life histories.

## Parental investment theory

### Infanticide

It is clear from the above discussion that child health outcomes are not solely related to genes or indeed exposure to pathogens, but can be greatly influenced by family circumstances, including decisions by parents in whom to invest (Hrды 1999). Parents have finite resources and make strategic decisions about how much to invest in any given child (Hrды 1999). In an extreme manifestation of maternal selectivity, Scheper-Hughes (1992) describes how women living in abject poverty on Brazilian sugar

plantations somehow disinvested in children they could not support. Despite the efforts of perplexed medical practitioners to help the children survive acute health crises if they could, the same children seemed to fall sick, fail to recover, and often died. In food-limited populations, parental investment is part of the trade-off between mother's body maintenance, her ability to keep a mate or attract a new one, and her ability to keep her other children alive. In many traditional human societies, including most hunter-gatherer societies, infanticide was common for children born into circumstances where the necessary parental and kin support was unlikely to be forthcoming. For example, in the Ache of Paraguay, children without living fathers were 3.9 times more likely to be killed by another Ache in each year of childhood; children of divorced parents were 2.8 times more likely to be killed during each year of childhood (Hill and Hurtado 1996: 437).

### Sex ratios

In developing the theory of sex ratio selection, Sir Ronald Fisher noted that all children have one mother and one father so the total reproductive success of males and females in a population is the same. It follows that if one sex becomes rare, individuals of that sex will have an advantage in terms of reproductive success. For example, if the breeding system is monogamous and the adult sex ratio is 1:2 (one male for two females), then males will have on average twice the reproductive success of females since half the females go unmated. If the mating system is polygynous, then each male will on average impregnate two females. Thus, regardless of the breeding system, the rare sex always has the reproductive advantage, and this produces a strong, frequency-dependent selective force that equilibrates only when the ratio of investment in the two sexes is 1:1 (Fisher 1930). The mechanisms of meiosis and the X-Y sex determination system of mammals reliably give rise to the approximately 1:1 sex ratio at birth, and these mechanisms may have evolved for Fisherian reasons. In many mammals, however, the 1:1 ratio is slightly adjusted by the uterine environment and the selective abortion of embryos of one sex.

Another nuance of sex ratio theory bears emphasis: it is the *total* investment in each sex that is generally equal rather than the *number* of each sex that is born (Fisher 1930). If the average cost of raising one sex through to independence is more than that of the other, then parents will on average raise to adulthood fewer offspring of the costlier sex (Fisher 1930). In humans and most mammals, the average male conceived is less costly than the average female conceived because males tend to die at higher rates in the juvenile period and death puts an end to parental investment; sex ratios at conception consequently tend to be male-biased. When one considers only the offspring who are successfully raised, on the other hand, males are on average more costly than females and sex ratios at breeding tend to be female-biased.

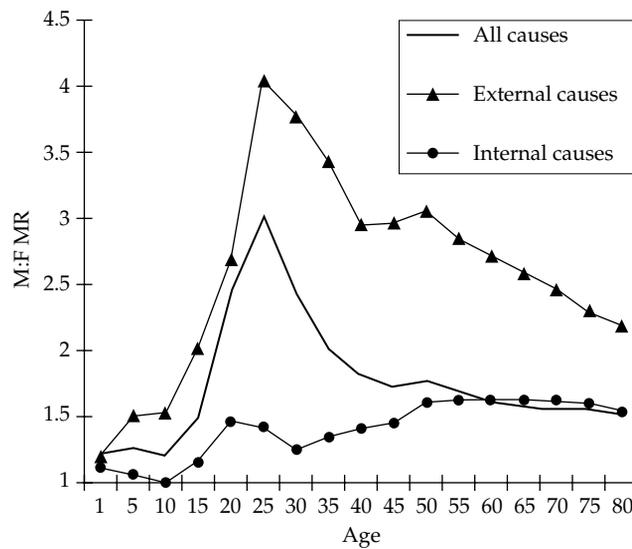
Behavioral ecologists have studied the cultural and ecological factors that contribute to the differential costs of raising boys and girls. For example, females are more costly in dowry societies in northern India (Das Gupta 1987). Females are also more costly in Inuit societies where male hunting is the primary source of food and females return fewer benefits to the household economy (Smith and Smith 1994). In these cases infanticide can occur and tends to be strongly female-biased. Moreover, if resources are more useful for males than females at attracting mates (which is true in most wealth-inheriting, polygynous, human societies), then parental investment of these resources will be predominantly male-biased (Trivers and Willard 1973). Sex-biased investment is frequently against females, but in some societies parents get a better return on their parental investment through daughters and treat them better than sons (Cronk 2000). For example, among the Mukogodo of Kenya, females tend to marry outside the ethnic group to higher status Maasai males, whereas Mukogodo males experience difficulty in attracting mates. Parents consequently favor daughters and girls are less nutritionally deprived and experience superior growth compared with boys (Cronk 2000). Levels of parental investment can also be influenced by birth order (Taylor 2005). For example, in some pastoralist societies, there is only enough wealth for a few sons to be supported into marriage; later born children are often left unmarried or marry very

late, and parents invest preferentially in their early-born sons (Mace 1996).

## Sexual selection theory

In humans and other mammals, mothers expend resources on gestation and lactation, whereas males sometimes donate only the sperm that fertilizes the egg. Although human males tend to do more paternal investment than the males of most primate species, humans often show a pronounced skew in the relative parental investment by mothers versus fathers (Trivers 1972; Lancaster *et al.* 1987). This skew arises from the fact that reproductive success in males is usually limited by the number of females that a male mates with, whereas additional matings usually do not increase reproductive success in females (Bateman 1948; Trivers 1972). Pregnancy and lactational amenorrhea in hunter-gatherer and traditional societies last about nine and twenty months, respectively, so if a female mated again during this time she would not get pregnant. Males on the other hand can greatly increase their reproductive success by copulating with many females in short order, so they tend to put more of their reproductive effort into securing extra matings (Trivers 1972).

Sexual selection refers to selection for traits (including behaviors) that increase mating success (Chapter 1); it is more intense in males because they compete against each other to mate with fertile females (Darwin 1871; Trivers 1972). Human females compete against each other to marry the best males, and that is what dowry competition is all about (Gaulin and Boster 1990), but the stakes are not as high. The range of variation in reproductive success in females is usually lower than in males. The average reproductive success of both sexes is the same, but in males one finds more extreme 'winners' and 'losers' in the reproductive gambit (Trivers 1972). Betzig (1986) describes the extreme harem sizes of despotic males, which sometimes numbered in the hundreds. Ghenghis Khan and his male kin employed such a successful polygynous strategy that 8% of all Asian males (sampled in 16 populations) can trace their Y chromosome to these twelfth-century Mongol rulers (Zerjal *et al.* 2003). For every man who gets



**Figure 9.3** The ratio of male to female mortality in the United States in 2000. From Kruger and Nesse (2006).

an extra fertile mating another man is disenfranchised, so there is fierce reproductive competition among males. Reproductive competition also exists among females, especially in polygynous families, but the intensity of competition is lower (Strassmann 2000, 2003).

### Higher mortality of males than females

Males have evolved to put more of their total energy budget into reproductive competition and less into health and longevity (see Daly and Wilson 1983: 298–9). Males who did not take risks to fight against other males for fertilizations left few descendants. Females, on the other hand, could take pregnancy almost as a given and direct more energy to somatic maintenance and repair. Risky behaviors that would leave their children motherless did not pay off. The greater intensity of sexual selection in males was a self-reinforcing process. Males took more risks, experienced more trauma, and had shorter life expectancies, which caused them to discount the future. They invested in traits that increased reproduction in the short term at the expense of the long term, intensifying male–male competition in early adulthood (reviewed in Kruger and Nesse 2006).

Even today, the greater intensity of sexual selection in males causes them to have higher mortality rates than females, with a peak difference in young adulthood (Wilson and Daly 1985). As shown in

Fig. 9.3, the ratio of male to female mortality (MR) in the United States in 2000 was always greater than 1, peaking at 3.01 at age 20–4 years (Kruger and Nesse 2006). The highest MR for a specific cause averaged across all ages was 4.7 for suicide, which also had the highest peak for any age group: 7.8 for ages 75–9 years. Next came non-automobile accidents (MR = 4.89) and homicide (MR = 4.35) in the age group 20–4 years. Diseases with high MRs were led by infectious disease (MR = 2.46) in the age group 45–9 years, followed by liver disease (including cirrhosis) and cardiovascular disease. In all circumstances except female infanticide and severe discrimination against women, excess male mortality is the prevailing pattern. For example, in the Ache of Paraguay, males died from accidents at twice the rate of females (Hill and Hurtado 1996). The peak in the MR at the time when males are entering into reproductive competition, and the well-known male–female difference in life span are the signature of sexual selection (Kruger and Nesse 2006). Sexual selection is also responsible for sexual dimorphism and the higher somatic maintenance costs of males (Bribiescas 2001; Campbell *et al.* 2001); their skeletal musculature alone accounts for 22% of basal metabolic expenditure compared with 16% in females (Elia 1992). In a study of men and women aged 17 to 81 years, resting metabolic rate was 23% higher ( $1,740 \pm 194$  kcal/day) in men than in women ( $1,348 \pm 125$  kcal/day) (Arciero *et al.* 1993).

All traits result from an interaction between genes and the environment (West-Eberhard 2003; Chapter 1), and the MR is strongly influenced by social factors. Individuals are more risk averse and will pursue strategies with long-term pay-offs if they perceive that their environment is favorable. In humans, the social environment and educational and economic opportunities are critical, and MRs are higher in disadvantaged groups (Singh and Yu 1996; Kruger and Nesse 2006). In regard to health, few aspects of a person's social niche are as important as marital status and marital satisfaction. In a study of American youth of both sexes aged 20 to 24 years, the hazard of death was 2.2-fold higher for divorced, separated, and widowed persons than for their married counterparts (Singh and Yu 1996). This result may reflect differences between those who marry and those who do not rather than the beneficial effect of marriage per se, but it did control for sex, income, education, race, residence, and immigration status. Married men are expected to decrease mating effort and to increase paternal effort and long term investments. As discussed by Bribiescas and Ellison (Chapter 7), testosterone plays a role in mediating the trade-off between mating and parenting in human males (Gray *et al.* 2002); testosterone declines after marriage and increases after divorce when a man resumes mating competition (Mazur and Michalek 1998). In birds, the testes regress outside the breeding season to spare the high costs of testosterone, which include the risks of territorial aggression and mate guarding (Daly and Wilson 1983: 100–2). High testosterone levels are advantageous for mating competition, but are costly in terms of impacts on immune function (Campbell *et al.* 2001) and longevity (Hamilton and Mestler 1969). In women, estrogen and progesterone are metabolically costly and contribute to reproductive cancers; but menopause, menstrual cyclicity, and hormonal suppression mitigate these costs (Chapter 7) (Eaton *et al.* 1994; Strassmann 1996; Jasienka *et al.* 2000; Ellison 2001: 168–213).

### Sexual jealousy and genital cutting

Like songbirds, human males engage in paternal care and expend considerable effort on

mate guarding, a behavior that protects against cuckoldry—a word derived from ‘cuckoo,’ a bird that lays its eggs in another bird's nest. Evolutionary ecologists define cuckoldry as paternal investment in genetically unrelated offspring. Sexual jealousy helps to defend paternity certainty and is the leading cause of marital violence (Daly *et al.* 1982; Daly and Wilson 1988). Female genital cutting, performed on about two million females per year, reduces female sexual pleasure so as to enhance sexual fidelity (Strassmann 1997). Tools include glass and razor blades (often nonsterile), and the practitioners are usually women who act on behalf of parents who feel that genital cutting is a requirement for securing an advantageous marriage for daughters. Where men prefer clitoridectomized women as marriage partners, the reproductive benefits of cutting may outweigh the reproductive costs. For example, among the Kassena-Nankana of Ghana, girls who had undergone genital cutting had nearly one child more than uncut girls, and this was mediated by an earlier age at marriage and first pregnancy (Reason 2004). Nonetheless the health costs can be considerable and can include infection, repeated urinary infections, obstruction of menstrual flow, infertility, and chronic pelvic pain (<http://www.womenshealth.gov>). Morison and co-workers (2001) found a higher prevalence of herpes simplex virus 2, a known risk factor for HIV infection, in cut than in uncut women in rural Gambia. Modern medical practitioners are increasingly coming into contact with patients at risk for genital cutting and may feel the pressure to let cultural relativism stand in the way of the need to forewarn these patients and their parents. Sexual selection theory elucidates the adaptive advantages for males (at the expense of females) and can unravel confusion created by ideologies whose root goal is male control of female sexuality.

### Summary

1. In order to fully exploit the insights that can be gained from evolutionary medicine, the medical community needs to consider how the genes interact with their environments during development. Patients are phenotypes; thus all medical conditions are a product of genes and the environment.

Under varying environmental conditions, the same genotype can lead to a wide array of phenotypes.

2. Natural selection has favored phenotypic plasticity because it promotes reproductive success by creating a better fit between the genotype and the environment. The genes give organisms the *capacity* for phenotypic plasticity, which means that organisms can be expected to respond to their environments in adaptive ways. In a nutshell, this is the evolutionary argument for expecting the flexible, circumstance-dependent behaviors of humans and other organisms to be fitness-promoting.

3. The cornerstones of evolutionary theory that guide the study of behavior include kin selection, life-history, parental investment, and sexual selection theory. This is a rich body of theory that can illuminate a wide variety of medical and public health problems, such as child abuse and homicide in step-families; deadbeat dads; attachment disorders; failure to thrive; female infanticide; excess male mortality from accidents, suicide and disease; risky behavior; immunosuppression; reproductive cancer; marital violence; and genital cutting.

4. Many of these problems reflect reproductive conflicts of interest *between* individuals, for

example, between parents and offspring, siblings, members of the same sex, and males and females in mating relationships. Other conflicts occur *within* individuals and involve life-history trade-offs: mating versus parental effort; offspring number versus quality; present versus future reproduction; and reproductive effort versus longevity. Conflicts of interest within and between individuals constrain natural selection and prevent the creation of a Panglossian world wherein adaptation is maximized at all levels simultaneously.

5. It is hoped that health professionals will explore the reproductive conflicts of interest that underlie many different kinds of medical situations; they will thereby tap into a valuable new way of understanding human health and disease.

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