



REVIEW

Evolutionary ecology of human life history

RUTH MACE

Department of Anthropology, University College London

(Received 8 February 1999; initial acceptance 25 March 1999;
final acceptance 9 September 1999; MS. number: RV-9)

The human life history is characterized by several unusual features, including large babies, late puberty and menopause, and the fact that there is a strong cultural influence on reproductive decisions throughout life. In this review I examine human life history from an evolutionary ecological perspective. I first review the evidence for life history trade-offs between fertility and mortality in humans. Patterns of growth, fertility and mortality across the life span are then discussed and illustrated with data from a traditional Gambian population. After outlining the stages of the human life course, I discuss two phenomena of particular interest in evolutionary anthropology, both of which are apparently unique to humans and neither yet fully understood. First, I discuss the evolution of menopause, the curtailing of female reproduction long before death. The evidence that this evolved because investment in existing children's future reproductive success is more important than continuing child bearing into old age is reviewed, along with data relating to the biological constraints that may be operating. Second, I discuss the demographic transition. Declining fertility at a time of increasingly abundant resources represents a serious challenge to an evolutionary view of human life history and behaviour, and is thus examined in detail. Parental investment in children in competition with each other may be key to understanding both of these unusual human phenomena.

© 2000 The Association for the Study of Animal Behaviour

Humans have big, but relatively helpless, babies, infant mortality is high, sibling rivalry is fierce, puberty is late and, for women, child bearing is rapid and dangerous, parental effort is arduous and protracted, and postreproductive life is long. Whilst many of these characteristics are common to the apes, many are exaggerated or unique in *Homo sapiens*.

Humans are so unusual in so many respects that it is hard to attribute some aspect of our behaviour or life history to some aspect of our ecology by comparison with other primates. An outstanding oddity is the size of the brain, which lies two to three standard deviations above the line predicting brain size from body size for primates (Pagel & Harvey 1989); and it is plausible (although far from certain) that many of the other unusual features of human life history relate back to this. The consequences of a large brain are both behavioural and physiological. In this review I concentrate primarily on those aspects of human life history that are behavioural and most related to our social system, but our social system has had a

powerful influence on the evolution of our physiology as well as our psychology.

Human behaviour is hugely influenced by culture, itself a by-product of our intelligence. So integrated are behaviour and culture that I use the two words almost synonymously in this review. We can decide when to mate and have children, how much to feed them, how long to live with them. These are either individual decisions or behaviour followed because we want to follow some cultural norm; most such decisions are a combination of both of these features, which are no doubt also influenced by genetics.

Amongst those studying the evolution of human behaviour, the emphasis differs as to which theoretical framework is most likely to help us understand why we do what we do. Evolutionary psychologists have taken a view that much of our behaviour can be understood as genetically adapted to an ancestral environment in which we existed as hunters and gatherers for most of our evolutionary history. This ancestral environment is often referred to as our environment of evolutionary adaptedness, generally proposed as a dry, African savannah. This model draws heavily on one of the first hunter-gatherer

Correspondence: R. Mace, Department of Anthropology, UCL, Gower Street, London WC1E 6BT, U.K. (email: r.mace@ucl.ac.uk).

groups whose life history was ever studied: the !Kung San of southern Africa (Howell 1979). These mild, monogamous, musical people, with carefully spaced children, provide an appealing candidate for the typical, ancestral human social unit. But the legends of !Kung life are faltering. Their famous 4-year birth intervals retreated to the more common 2.5–3 years when !Kung were treated for sexually transmitted diseases (Pennington 1992), as did those of all the other populations in northwestern Botswana. And in Cavalli-Sforza et al.'s (1994) examination of human population history, the !Kung are described as an unlikely candidate for an ancestral African group, that might even have migrated into Africa from Asia. Subsequent studies of other hunter-gatherers have exposed what any behavioural ecologist might have suspected, which is that there is no clear case for a typical human ecology. In a recent study of the Ache of Paraguay (currently the most thorough examinations of forager life history), Hill & Hurtado (1996) described a group that, in many ways, is much more likely to characterize ancestral humanity. The Ache had far less exposure to nonforaging groups than the !Kung. Forest dwellers, they lived in fierce isolation until 1972, when they were devastated by epidemics caught from missionaries. Those that survived had to retreat to reservations. Their story revealed a life of hardship, violence within and between social groups and rapid reproduction. Infanticide and geronticide were common, family groups were unstable and few individuals lived long enough to contribute much to the social unit in postreproductive life. Constant warfare between groups, with populations sometimes almost wiped out, sometimes expanding rapidly into new areas, could easily be the circumstances in which our life history evolved.

Some evolutionary psychologists (e.g. Symons 1979) have argued that the origin of agriculture, which fuelled population expansion, was so recent that evolution has not had enough time to change our behaviour since then, and thus there is little point in studying the fitness consequences of any behaviour in societies other than hunter-gatherers. However, there is evidence for genetic adaptation in humans since the origin of agriculture; for example, the ability to digest lactose as an adult has evolved as an adaptation to dairying in groups that have been keeping cattle for less than 10 000 years (Simoons 1978; Holden & Mace 1997). It can be argued, convincingly, that workloads, reproductive experience and many other aspects of life history did not change nearly as much in the transition between foraging and peasant farming as they have done much more recently with the demographic transition to small family size (Strassman & Dunbar 1999), a topic I return to below.

Given that we do not know what our ancestors did, we cannot compare ourselves very meaningfully with other primates, and humans are generally not amenable to experimental manipulation, then we are left with an examination of the ecological and social correlates of individual and cross-population variation in human life history. Thus the methods of behavioural and evolutionary ecology are likely to be important. For human beings, the cultural environment is as much a given as any other

part of our environment, so the tools of behavioural ecology have to be applied in a framework in which the environment includes culture. Some evolutionary anthropologists have examined cultural evolution by modelling the transmission of cultural units or memes as distinct heritable units subject to selection, albeit with different transmission characteristics from genes (e.g. Boyd & Richerson 1985). Whilst recognizing that culture is rather different from other aspects of the environment, this approach has not produced many opportunities for the empirical testing of hypotheses. This contrasts with the behavioural ecological approach, which has spawned an expanding body of literature on human behavioural adaptation.

In this review, I illustrate many aspects of human life history with data from a west African village collected between 1950 and 1975. This data set is one of the most complete records of the demography of a natural, food-limited, human population from Africa, if not from anywhere. It was collected, in real time, as part of a long-term medical research project, based in a Gambian village where the population were reliant on agriculture and suffering high mortality. I choose this population to illustrate an evolutionary ecological view of human life history, not because it has any claim to being ancestral, but only because it is a well-documented, traditional population that is as likely to be characteristic of humanity as any other.

TRADE-OFFS IN LIFE HISTORY

Figure 1 illustrates the essential features of the human life history: growth, mortality and fertility. A fundamental assumption of life history theory is that trade-offs exist between energy expended on growth and factors influencing mortality on the one hand and reproduction on the other (Williams 1957; Roff 1992; Stearns 1992). The costs of reproduction may be paid in terms of energy being diverted away from body repair and maintenance (Kirkwood & Rose 1991) and reducing investment in immunological competence. Evidence for trade-offs between reproductive effort and life span has been gathered from experimental manipulation in numerous animal species (reviewed in Roff 1992). An obvious problem with gathering such evidence from humans is that researchers have had to rely on phenotypic correlations or 'natural experiments'. Phenotypic correlations are problematic, because heterogeneity in a population can obscure true relationships between life history variables. For example, if individual women are reproducing up to their own capacity, then healthier women have larger families and potentially greater longevity, but if that additional reproduction shortens life span, then no correlation between family size and longevity will emerge. Notwithstanding these problems, immediate costs both in terms of maternal mortality risk and also nutritional stress after reproduction have been shown in malnourished populations (Tracer 1991). Lund (1990) found that women in Norway with fewer than four children live longer than those with more than four children. Westendorp & Kirkwood (1998) used historical

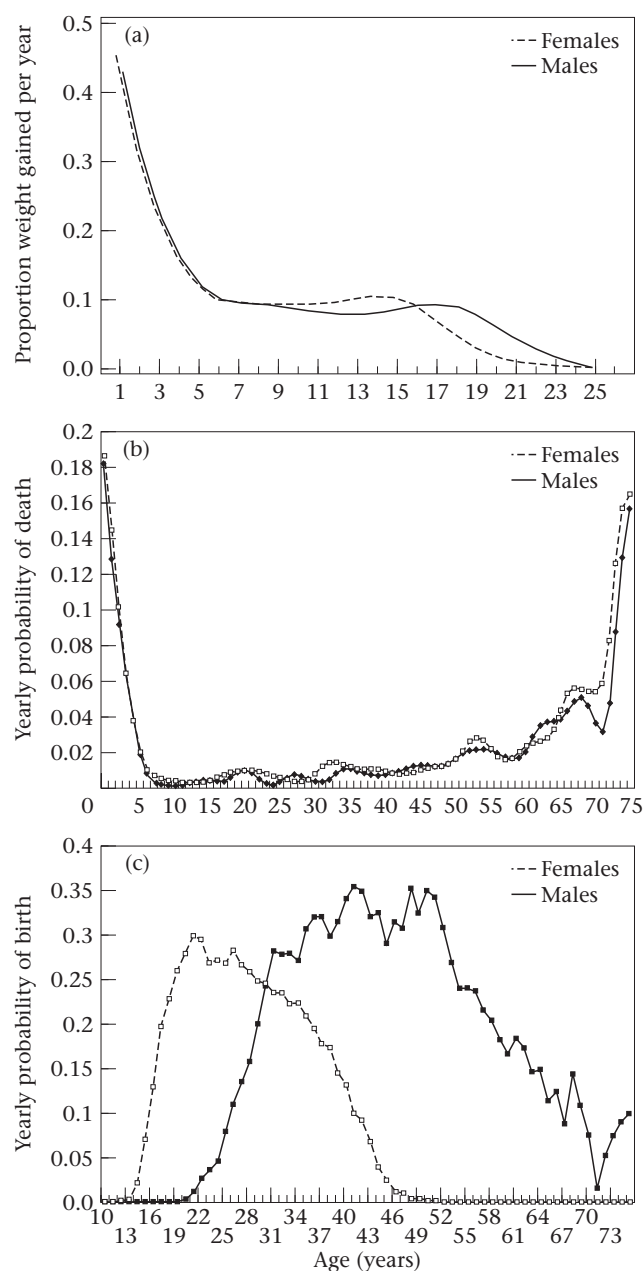


Figure 1. Cross-sectional data on the life history of rural Gambians, based on data collected by Sir Ian McGregor from Keneba and Manduar villages between 1950 and 1975. (a) Average annual weight gain as a proportion of total weight, between years of age and 25 years of age for males and females. (b) Annual mortality hazard for males and females over the life span. (c) Age-specific fertility (number of live births per year) for males and females over the life span (3-year running means).

data (from 1500 to 1875) to show that faster child bearing in women of the English aristocracy was associated with a shorter life span among those reaching advanced ages. They also found that late reproduction was associated with longevity, also shown by [Perls et al. \(1997\)](#), which they interpreted as evidence of a genetic trade-off between reproduction and longevity. It should be

noted that these effects are rather subtle, and it is not clear that they are operating at biologically meaningful levels.

With respect to assessing the role of immune function in life history, most of the relevant research on humans has taken a different direction from that done on other animals. This is due to the availability of data documenting variation in fetal nutrition, providing natural experiments which appear to show that gestation is a critical time for programming immune function in later life. [Barker \(1994\)](#) has shown that poor nutrition in the womb, caused either by serious food shortages for mothers or medical complications during pregnancy, is associated with skinny babies and greatly increased risk of degenerative disease in late adulthood (such as diabetes and heart attack). [Moore et al. \(1997\)](#) used marked seasonality as a natural experiment to show that mothers in the third trimester of pregnancy in the hungry season in the Gambia had children that were more likely to die of infectious disease when adult. Whether diversion of energy away from the immune system in adult life mediates costs of reproduction has yet to be established.

Whatever the precise mechanisms of the costs of reproduction are, women around the world are certainly well aware of them. [Hill \(1997\)](#) recounted how Gambian women describe the costs of reproduction as they see them, through the Mandinka concept of *faaso*:

the basic idea is that women have a certain capacity at birth or marriage, that is depleted steadily as women experience a number of reproductive events, and that once depleted, it cannot be totally replenished, although some may be rebuilt through rest and a good diet. . . . A woman with little *faaso* left is "old." Very few men want women with low *faaso* reserves, so for a woman it may be prudent, if a marriage is rocky or the husband sickly, to conserve some *faaso* in case a new marriage is imminent. (Copyright 1997 The University of Chicago.)

Pure sociobiology. It is the optimal expenditure of *faaso* through life that is the challenge of human life history. Trade-offs are involved at every stage: trade-offs between growth and reproduction, between one child and another, between children and grandchildren. Life history theory is the only theoretical paradigm with the potential to predict how natural selection should resolve these trade-offs.

THE LIFE COURSE

Birth and Infancy

Birth is difficult and painful in humans because the baby is large and our upright posture necessitates a stiff pelvis. For the majority of mammals, brain growth slows at birth, but in humans, the skull is not fully hardened at birth, to ease delivery, and the brain grows rapidly after birth for about a year, reaching adult size in about 7 years ([Bogin 1999](#)).

Delivery is still risky for both mother and baby. Maternal mortality varies enormously around the world, reaching a peak in hospitals with poor hygiene, where delivery

can be more dangerous than at home. In countries with no effective modern medicine, the risk of death in childbirth outside hospital is less than 1% per birth, but follows a J-shaped function, that is, it declines after the first birth, and then rises again in high-parity women. The overall rate may be less than our fear of childbirth would lead us to expect, but, as adult mortality in humans is low, a less than 1% risk of maternal mortality per birth typically translates into between 0.25 and 0.33 of all deaths of women of reproductive age in natural fertility populations (see Mace & Sear 1996 for African examples). Female mortality often exceeds that of males during their 20s and 30s, for this reason. The provision of antibiotics and facilities for safe Caesarean section markedly reduce this risk (Graham 1991), and when these are available maternal mortality is negligible.

Risks for the baby are far higher. Except with the best medical care, perinatal mortality risk rarely falls below 1%. Some of this mortality may be genetic defects which are fatal only after birth. In the Gambian example in Fig. 1, the opposite end of the spectrum is illustrated: 7% of all infants born alive died within 1 month. Body weight is a strong and consistent correlate of an infant's chance of surviving its first year. Weaning is a hazardous time, as infants are exposed to less nutritious food and unclean water. The earlier children are weaned, the higher is infant mortality. The most common reason for weaning is a subsequent pregnancy; and the evidence that closely spaced births greatly increase infant mortality is overwhelming (Hobcraft et al. 1983; Alam 1995; Bohler & Bergstrom 1995). Older siblings then compete for food (LeGrand & Philips 1996).

Human babies are also at risk from infanticide, or neglect leading to reduced survival. The classic scenario outlined for numerous mammals of infanticide by incoming males, so as to redirect a mother's parental effort towards the new males' future offspring, is a serious risk to children under 2 in our own society (Daly & Wilson 1985). Voland (1988) found statistical evidence from 18th-century Germany that women who were widowed when they were young might have been depressing the survival chances of their young children in order to enhance their prospects of remarriage. Again, something similar appears in our own backyard (Daly & Wilson 1996). Abandonment of the mother by her husband is frequently associated with infanticide, often at birth (e.g. among the Ache; Hill & Hurtado 1996). Sex preferences can also cause significant sex biases in infant and child mortality. These biases can be against girls (as often found in patrilineal societies, particularly in Asia) or boys (particularly in matrilineal societies, such as in southern Africa; e.g. Harpending & Pennington 1991). Children of the least favoured sex who have older siblings of the same sex are at particular risk (DasGupta 1987). The majority of these patterns that indicate parental influence in childhood mortality have been discerned by careful statistical analysis of demographic data rather than by interviews with parents. However, when economic conditions and levels of kin and paternal support are very poor, mothers do sometimes admit to their unwilling compliance in

infanticide by neglect, as Scheper-Hughes (1992) described in Brazilian shantytowns.

Faced with the hazards of babyhood, there is little the baby can do about it except grow up as fast as possible (Fig. 1a). As children grow, they require less intense parental effort, and as they escape into the oasis of childhood they appear to be less at risk of mortality in general (Fig. 1b).

Childhood and Puberty

Childhood is not unique to humans, something similar being found in other apes (Perreira & Fairbanks 1991), but in humans it is especially prolonged. Childhood is generally assumed to be about intellectual and social rather than physical development (Bogin 1999), although there are some dissenters from this view (Blurton-Jones et al. 1999). Hard evidence that what we learn in childhood contributes to our fitness is conspicuous by its absence. Catch-up growth, shown by children recovering from illness or a period of malnutrition, illustrates that a much faster growth rate than that shown is physiologically possible. But an adult-sized, fully developed 5-year-old is a scary thought, and it is doubtful that they would be particularly successful in the competition for resources or mates with 20-year-olds. Better that a period of learning, or simply waiting, is protected in a state of lower nutritional requirements, less threat to adults and low mortality. Along similar lines, Haig (1999) described childhood as a strategy to extract more parental investment.

When children reach puberty, they spurt in growth to at or near their full height. This adolescent growth spurt is uniquely human. Figure 1a shows average weight gain for children of each age, but individual growth curves would show pronounced spurts, which here are averaged out. Growth spurts are more pronounced in well-nourished than in malnourished populations, such as this Gambian case. Males achieve greater, average adult height than females in all populations studied, although cross-population variation in sexual dimorphism in stature is probably related to sex-biased parental investment experienced during childhood (Holden & Mace 1999). Female growth spurts are at a younger age than male growth spurts, and tend to occur before the child becomes fertile, perhaps because the consequences of pregnancy whilst being underdeveloped would be so serious for girls. In particular, growth in the width of the hips is associated with the onset of fertility (Bogin 1999). Early maturation can also be hazardous for boys: Hill & Hurtado (1996) described how Ache boys are initiated once they start making serious advances towards girls, making them eligible targets in club fights with adult males.

The onset of puberty, which is coincident with the slowing of growth in females, appears to show great plasticity according to environmental circumstances. Stearns & Koella (1986) illustrated how there is neither a fixed height nor age at menarche, but a reaction norm exists, where malnourished females will reach menarche at a greater age but a lesser height. A secular trend towards

earlier puberty in well-nourished populations has been noted everywhere.

Mating and Marriage

In human societies, mating patterns are frequently legalized in marriage, and marriage patterns are highly diverse. The majority of cultures show patrilocal marital residence (females move from the natal group to live with their husband's family). Seielstad et al. (1998) used genetic evidence, that spatial variability in Y chromosomes appears to be less than in mtDNA or X chromosomes, to argue we are essentially patrilocal, that is, women are more likely to migrate. Our closest primate relatives, chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*, show female dispersal, which has been used to argue that patrilocal residence is ancestral in humans; however, given 5 million years of evolution, and the diversity of marriage patterns within our own species, we should not take this as a certainty. Hunter-gatherers show diverse lineality or no lineality at all; and the origin of defensible and heritable wealth changes everything. A significant minority of human groups show matrilineal descent, where wealth (such as land) is inherited down the female line, and mothers live with their daughters, who inherit their fields; marital residence is matrilineal. Men have little in the way of personal possessions, but are meant to pass them on to their sister's children, not their own children (Schneider & Gough 1961). Marriages are typically unstable; because a male's investment in his wife's children is low, the emphasis on marital fidelity is weak. However, the emergence of valuable, heritable wealth, such as livestock, that needs to be defended against theft by men, has been associated with patrilineality (Engels 1884; Aberle 1961; Mace & Holden 1999). Here wealth is passed from father to sons, marital residence is patrilocal and the emphasis on marital fidelity is strong. Wives, frequently purchased with brideprice, become possessions who are not free to leave, as they would lose wealth and children if they did.

The extent to which marriage patterns reflect mating patterns is unclear. It is difficult to get direct data on paternity uncertainty in humans for ethical reasons, but several estimates tend to settle at around 10%. An intriguing method of estimating paternity uncertainty has been used by Gaulin et al. (1997) and Euler & Weitzel (1996), who used kin selection theory (Hamilton 1964) to show that matrilineal relatives invest more in children than patrilineal relatives in western Europe and the U.S.A. in proportions consistent with paternity uncertainty between 9 and 15%.

The physical attributes that are considered attractive in mates have been extensively reviewed elsewhere (e.g. Buss 1989; Barber 1995), and I will not go into them again here, but two clear and consistent influences are age and wealth. It is clear from sex differences in fertility through the life course that females should be most in demand as marriage partners when young, but males can achieve high fertility even when quite old (Fig. 1c). The extent to which this is true again depends on the socioeconomic circumstances in which people live. A polygynous mar-

riage system combined with patrilineal ownership of resources (as seen in this Gambian case) means that old men can have young wives if they own the resources to support them and their children. It may be advantageous for young women to marry older, polygynous men if they are wealthier; for example, Josephson (1993) used historical demographic records to show that polygynous Mormon wives in 18th-century Utah had more grandchildren than monogamously married women. Where inherited resources contribute strongly to future reproductive success, marriage can be delayed and competition between siblings can be shown to reduce directly the reproductive success of those inheriting less (Johansson 1987; Low 1991; Mace 1996a).

The Pace of Child Bearing

Reproductive scheduling in human females has characteristics strikingly different from that of other great apes. First, 2.5–3.5-year interbirth intervals appear rather short for our body size (for example, gibbons, *Hylobates* spp., have 3-year interbirth intervals, chimpanzees 4–5 years, orang-utans, *Pongo pygmaeus*, nearer 8 years). Second, reproduction terminates about half-way through adulthood with the menopause, a programmed senescence of the reproductive organs perhaps 20 years before the equivalent senescence is seen in the rest of the body. The biological ability of women to reproduce again after each birth is dictated by a number of energetic influences on ovulation, including breast-feeding patterns and workload (Ellison 1994). The great majority of births are singletons, although twinning rates increase with age, and persist at high enough levels that twinning must be selected for in some circumstances, despite twin mortality being high. Gabler & Volland (1994) calculated that, in the circumstance of 18th-century Germany, twinning led to increased long-term fitness (number of grandchildren) only if both twins were girls. However, mothers of twins are often especially fertile individuals (e.g. Lummaa et al. 1998) and twinning might be maintained as a pleiotropic side-effect of this beneficial trait.

Birth intervals tend to increase with age even before menopause is reached. This may be part of the ageing process, or an evolved response derived from sibling competition. There is evidence from some societies that slowing of reproduction is associated with achieving the desired family size. For example, the absence of a son in the family in a patrilineal society is associated with continued reproduction (e.g. Nath & Land 1994; Mace & Sear 1997).

The relatively rapid pace of child bearing in the first half of adulthood leads to a number of offspring at different stages of dependency, needing to be cared for simultaneously. The ability to achieve such a family has been attributed to mothers being able to co-opt help with childcare and nutrition from other family members. Male provisioning, which is not seen in other primates, may enable high birth rates in human females (Hill 1993), but equally postmenopausal females may be the source of that additional, energetic contribution to the family (Hawkes et al. 1997). Whoever was the greatest influence

is not agreed upon, but it seems unlikely that rearing a human family was ever a job for mothers alone. Childcare might have been a responsibility for all but the youngest ages, whether as an older sibling, a parent, or a grandparent. As the extended family disperses in the modern era, parenthood becomes a hectic time of life, bounded on either side by long periods filled with increasingly elaborate educational and recreational activities or thumb twiddling.

THE EVOLUTION OF MENOPAUSE

Menopause may have evolved precisely so that older women could assist their children reproduce rather than continue to do so themselves, a theory known as the grandmother hypothesis (Williams 1957; Hamilton 1966). If females dispersed at marriage, then it may be necessary to argue the grandmothers were helping their daughters-in-law rather than their daughters. The genetic relatedness to the child of a daughter-in-law and to the child of a daughter will differ by the extent to which paternity is uncertain, and somehow the notion of a benign mother-in-law rings a little less true (Skinner 1997 claimed that the early death of a mother-in-law increased the life span of Japanese women). Thus the issue of the evolution of the pace of child bearing and the evolution of menopause are linked with each other, and with the issue of what our ancestral family structure was like.

Evidence that women can increase their number of grandchildren by an amount sufficient to outweigh the loss of their own reproductive opportunities is mixed. Simple models have failed to make forgoing reproduction in favour of grandmothers appear evolutionarily stable (Hill & Hurtado 1991, 1996; Rogers 1993). However, these models are based on the assumption that the risks of reproduction and the benefits of grandmothers have to outweigh the benefits of continued reproduction at the rate of a young woman, which ignores a huge range of costs and benefits that alter with age. Shanley (1999) has developed models of human female life history in which inevitable, generalized biological senescence is included; here the criteria favouring menopause emerge as far less stringent. The risk of maternal mortality is a key parameter in all these models, because this is what would deprive existing children of maternal care if fertility continued into old age. Maternal mortality risk has generally been assumed constant, but in fact it rises exponentially with age (Loudon 1992), as does neonatal mortality. Data from maternity hospitals in the U.S.A. and the U.K. in the 1930s show that the causes of maternal death that accelerated with age were related not to infection but to haemorrhage and a wrongly positioned placenta, possibly suggesting a role for reduced muscle strength and tone rather than reduced immunocompetence. In older women, the womb is unable to contract to prevent blood loss as effectively as in younger women, a problem now anticipated with ergometrine injections routinely administered just after delivery. Possibly, the combination of our large babies and the rapid reproductive rate that our social system allows imposes very high risks on continuing reproduction into old age. If these risks were to

accelerate further with age, as is not unlikely given the multifactorial nature of ageing, surviving a natural delivery in old age could become highly unlikely and the termination of reproduction by 50 would need virtually no other explanation.

Hawkes et al. (1997) argued that our reproductive period is not especially short, because it fits with a more general primate pattern (Charnov 1993), and that a long postmenopausal life span is the derived character that requires explanation. If true, again, the fitness benefits of grandmothers would not have to be so great for that to evolve (although this argument does not explain why men also have typically similar longevity to women but without male menopause). Hawkes et al. (1997) found that Hadza (forager) children who had a postmenopausal relative in their family group (albeit a very small sample) were fed by them and were better nourished than those that did not. The grandmaternal contribution appeared to be especially important when the child's mother had another baby. Hawkes et al. stressed the importance of tubers, which are hard for children to extract and process, and appear to be far more important in the diet than meat. Blurton-Jones et al. (1999) argued that grandmaternal help may be responsible for making early weaning possible in humans.

Quite apart from the risk of maternal mortality discussed above, there are a number of general and specifically human reasons why family sizes should not get too large. Only a small proportion of births are to women over the age of 40 in any society, even though menopause is nearer 50 (Wood 1994). Both Hill & Hurtado (1996) and Rogers (1993) noted that menopause would be much more advantageous if other costs paid by existing children were included. Competition between siblings for parental investment is one such factor. Whilst it is not clear that the effects of sibling competition on mortality are sufficient to curtail reproduction, there may be effects of such competition on future reproductive success that are. In earlier papers (Mace 1996b, 1998), I modelled optimal reproductive scheduling when siblings compete for parental wealth, when that wealth influences their future reproductive success. The models show that it is very rarely optimal for women to have the maximum fertility; thus, over a wide range of realistic cases, the cost of menopause would have been virtually zero. Competition for food, status, territories, breeding opportunities, kin support, or *faaso*, could all follow similar dynamics making large families show diminishing returns. Thus only small biological costs of maintaining female fertility beyond 50 could favour menopause.

In such circumstances, the benefits of parental and grandparental solicitude would not have to be very great to maintain an extended life span. And the list of possible benefits is long. Figure 2 shows data from The Gambia which suggest just some of these benefits. A living mother appears to be associated with age at first reproduction in her daughters being brought forward by about 1 year (Fig. 2a), and the babies born are more likely to survive if their maternal grandmother is alive (Fig. 2b). This preliminary analysis of the survival of first-born children suggests that the benefits of a living, maternal grandmother appear

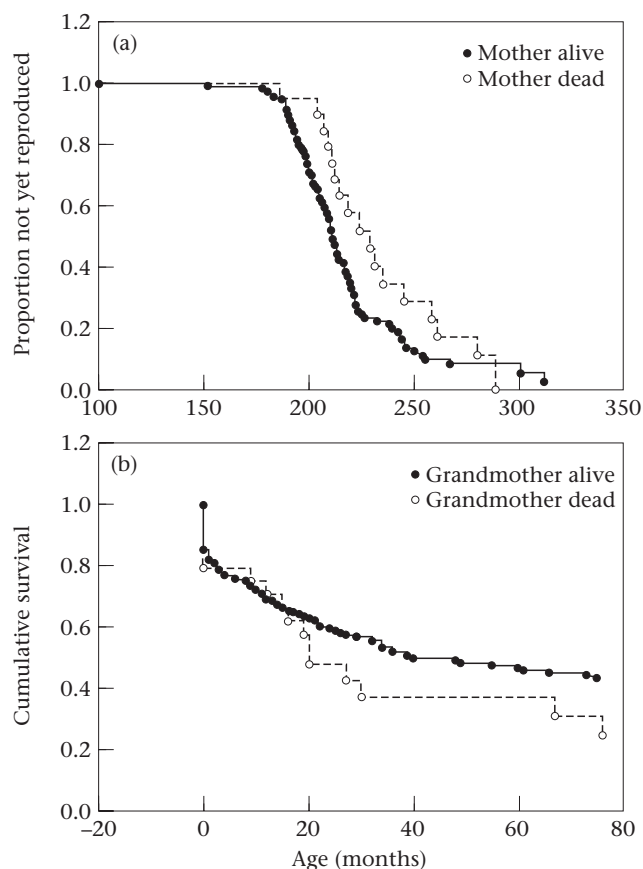


Figure 2. Kaplan-Meier plots of the first births to women of known age, from the villages of Keneba and Manduar, The Gambia, between 1968 and 1975. (a) Proportion of women not yet reproduced as a function of age in months, according to whether their mothers were alive or dead at the time of that birth, or in 1975 if not yet reproduced. (b) Survival of first-borns, as a function of age in months, according to whether their maternal grandmothers were alive at the time of their birth.

after the first 18 months, a pattern that is consistent with the hypothesis that these grandmothers are also contributing to feeding their grandchildren after weaning. Married women tend to live with patrilineal kin in this case, but usually not at great distances from their maternal home. The long-term benefits of earlier reproduction in daughters could be even greater, having benefit for all her future children and their children, making the fitness benefits of caring for existing daughters potentially overtake the risk-associated benefits of another late-in-life baby.

THE DEMOGRAPHIC TRANSITION

The most profound change in human life history has occurred recently, and it is cultural. About two centuries ago, during a period of very rapid population expansion, fertility in Europe and North America started to decline, along with mortality. This occurred in Asia and South America much later, and has recently started in Africa (Cleland 1995). The progress of this demographic and

health transition is not exactly the same in each region, and there are populations where it has not occurred at all; but there are sufficient similarities around the world to define a phenomenon in need of an explanation. An explanation for the demographic transition is of particular interest to evolutionary anthropologists, because a reduction in family size at a time of abundant resources presents a serious challenge to an adaptive view of human behaviour and life history. Insufficient time has elapsed for us to adapt genetically to some aspects of our modern life history. Our low reproductive rate, whilst relieving us of some old, medical problems, is presenting us with new ones, possibly including reproductive cancers. But reproductive decision making is plastic in traditional and modern societies, and it is therefore interesting to examine how such an evolved psychology could have produced such a consistent trend towards small family size.

Evolutionary ecologists are familiar with the notion that fertility might be reduced by some quantity/quality trade-off, going back to Lack (1968). Homogeneous populations, such as those usually studied by anthropologists, frequently show a positive correlation between wealth and reproductive success, as predicted from evolutionary ecological theory (e.g. Irons 1979; Borgerhoff-Mulder 1987; Mace 1996a). However, large, heterogeneous populations studied by demographers typically show a negative correlation between wealth and reproductive success. I have explored this paradox by using a state-dependent, dynamic optimality model to predict both optimal family size and the optimal amount of wealth to allocate to each child at the end of the parents' reproductive lives, when wealth inherited from parents was considered an important determinant of future reproductive success (Mace 1998). The two variables are related, because wealth spent on rearing children is not available for their inheritance. The important fact that wealth itself has the potential to generate more wealth was incorporated in the model. Optimal was defined as maximizing number of grandchildren. Three variables frequently associated with demographic transitions were varied in the model: extrinsic mortality risk; risk of drought (which influenced the productivity and reliability of the subsistence base); and the costs of rearing children. The model showed that the mortality risk, whilst having a strong influence on the number of births, had virtually no effect on optimal family size or on the amount of wealth allocated to each child. Alleviating the risk of drought predicted increased family size and reduced the inheritance given to each child, making the average family in the population poorer. Increasing the cost of rearing children was the only variable that produced results with the characteristics of a demographic transition: optimal family sizes fell, and the optimal wealth allocated to each child rose, making the average family in the population wealthier. These results match the evidence on the proximate demographic responses of people faced with environmental change. Free medical care has been available in the Gambian village of Keneba since 1975, which has dramatically reduced mortality, but there is no sign of the onset of a demographic transition (Weaver & Beckerleg 1993). Contrast this with examples of virtually instant

shifts in fertility observed when economic costs and benefits relevant to rearing children are altered (Hoem 1992; Conrad et al. 1996).

The model offers some insight into why a negative correlation between wealth and reproductive success is commonly observed. Within each model population, wealth was positively associated with reproductive success, but those model populations that had the poorest families also had the largest family sizes. If heterogeneous populations represent subpopulations, each experiencing (or believing they experience) different costs and benefits associated with investing in children, then a decoupling or negative relationship between wealth and family size might be observed. Hubback (1957, data reprinted in Mace, *in press*) presented an example from a somewhat homogeneous, privileged group of women in a post-transition society: British women who graduated from English universities in the 1930s and 1940s. She noted that wealth correlated positively with reproductive success. The standard of degree obtained by these women also correlated positively with their future fertility. This latter finding is intriguing as education is general associated with low fertility; but, again, this may be conflating cross-population and individual responses. Kaplan (1996) developed the idea of 'embodied capital', a term used to encompass all those benefits that parental effort can invest in children that might show long-term benefits. These benefits could be in terms of educational achievements, earning capacity, health or fertility. Whilst our psychology might favour increasing the quality of our offspring, whether that translates into reproductive success in the modern world is not clear. Kaplan et al. (1995) surveyed a contemporary sample of New Mexican men and found that those born into smaller families had greater educational achievements and earning power, but this did not translate into higher fitness. However, these data covered a period of economic and population expansion: that extra embodied capital might have paid better fitness returns in a stable population, where competition is more intense.

The majority of evolutionary ecologists are not in a position to study the historical process of behavioural change in populations, in the way that human evolutionary ecologists frequently are. This necessitates investigating the mechanisms associated with adaptation, and the time course over which they operate. Here studies from psychology, economics and other social sciences, which are beyond the scope of this review, intersect with studies on human fertility. But the onset of the demographic transition cannot be consistently attached to a particular biological, ecological or economic variable. It may be that the notion of high parental investment in each child is best thought of as a meme (*sensu* Dawkins 1976) that is spreading around the world, which is especially successful in certain circumstances. A careful analysis of fertility decline in France (Bonneuil 1997), which experienced the first and best-known demographic transition, shows how smaller families, presumably associated with higher parental investment in each child, spread from centres of sophistication over time. In remote areas, fertility decline came later, but once it started, proceeded

more rapidly. No simple, socioeconomic correlate predicts its spread, except perhaps distance from the epicentres.

Competition must be key. Certainly it is appealing to our psychology to invest in our children so that they can compete successfully against their peers, no doubt for good evolutionary reasons. Children in villages ultimately compete with those in other villages, in other cities, even in other countries, as populations become more mobile; they compete for exam results, for jobs and for mates. Once some of the population invest heavily in their offspring, others will follow. Having just upgraded my computer so that my 4-year-old can keep his computing skills comparable with others at his nursery, I can attest to the fact that this process starts young. When costs are viewed in terms of competition between children rather than the simple costs of subsistence, then it is possible to imagine that we are not as far removed from resource constraints on reproduction as our lifestyles make it appear. Where wealth is clearly abundant, time may be the resource that parents cannot allocate to their children in the quantities that would be optimal.

CONCLUSION

I have tried to illustrate how approaches from evolutionary ecology contribute to our understanding of our own lives. Whilst it would be tempting to relate all the strange attributes of the human life history back to one single effect (such as our big brain, or low adult mortality, or some aspect of our social system or diet), one lesson from studies in life history is that different traits are subject to different selection pressures. It is the combination of selection pressures influencing mortality and fertility that will favour a particular life history strategy, and models reveal that small changes in these selection pressures can have large effects on the optimal life history. Even in closely related species, different trade-offs appear to emerge as important. More studies will reveal the variation across cultures in human life histories, and in the trade-offs that are observed. Over time it will become apparent whether or not any consistent patterns emerge.

Evolutionary ecologists came late to the study of human fertility, mortality and growth. Medics, social anthropologists, psychologists, demographers and economists got there first, and have not always welcomed the newcomer; but they have not solved, nor even identified, all the interesting problems that human life history evolution presents. The paradigm of evolutionary ecology brings a new perspective, a new tool kit and new investigators to this unfinished task.

Acknowledgments

My research is funded by the Royal Society and the Wellcome Trust. Data from The Gambia were collected by Sir Ian McGregor, as part of a long-term collaboration between the MRC and the Gambian government. I thank Rebecca Sear for help preparing the figures, and all those

in the Gambia life history research project, Nadine Allal, Tom Kirkwood, Rebecca Sear, Daryl Shanley, Fiona Steele and Andrew Prentice, for helpful discussions, and Richard Sibly and another referee for providing very helpful comments on the manuscript. I am grateful to The University of Chicago for permission to use the extract from Hill (1997).

References

- Aberle, D. F. 1961. Matrilineal descent in cross-cultural perspective. In: *Matrilineal Kinship* (Ed. by D. M. Schneider & K. Gough), pp. 655–730. Berkeley: University of California Press.
- Alam, M. 1995. Birth-spacing and infant and early childhood mortality in a high fertility area of Bangladesh: age-dependent and interactive effects. *Journal of Biosocial Science*, **27**, 393–404.
- Barber, N. 1995. The evolutionary psychology of physical attractiveness: sexual selection and human morphology. *Ethology and Sociobiology*, **16**, 395–424.
- Barker, D. J. P. 1994. *Mothers, Babies and Disease in Later Life*. London: BMJ Publishing.
- Blurton-Jones, N., Hawkes, K. & O'Connell, J. F. 1999. Some current ideas about evolution of the human life history. In: *Comparative Primate Socioecology* (Ed. by P. C. Lee), pp. 140–166. Cambridge: Cambridge University Press.
- Bogin, B. 1999. *Patterns of Human Growth*. 2nd edn. Cambridge: Cambridge University Press.
- Bohler, E. & Bergstrom, S. 1995. Subsequent pregnancy effects morbidity of previous child. *Journal of Biosocial Sciences*, **27**, 431–442.
- Bonneuil, N. 1997. *Transformation of the French Demographic Landscape 1806–1906*. Oxford: Clarendon Press.
- Borgerhoff-Mulder, M. 1987. On cultural and biological success: Kipsigis evidence. *American Anthropologist*, **89**, 619–634.
- Boyd, R. & Richerson, P. J. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Buss, D. M. 1989. Sex differences in human mate preferences: evolutionary hypotheses testing in 37 cultures. *Behavioural and Brain Sciences*, **12**, 1–49.
- Cavalli-Sforza, L. L., Menozzi, P. & Piazza, A. 1994. *The History and Geography of Human Genes*. Princeton, New Jersey: Princeton University Press.
- Charnov, E. L. 1993. *Life History Invariants*. Oxford: Oxford University Press.
- Cleland, J. 1995. Obstacles to fertility decline in developing countries. In: *Human Reproductive Decisions* (Ed. by R. Dunbar), pp. 207–229. London: MacMillan.
- Conrad, C., Lechner, M. & Werner, W. 1996. East German fertility after unification: crisis or adaptation. *Population Development Review*, **22**, 331–358.
- Daly, M. & Wilson, M. I. 1985. Child abuse and other risks of not living with both parents. *Ethology and Sociobiology*, **6**, 155–176.
- Daly, M. & Wilson, M. I. 1996. Violence against stepchildren. *Current Directions in Psychological Science*, **5**, 77–81.
- DasGupta, M. 1987. Selective discrimination against female children in rural Punjab. *Population Development Review*, **13**, 77–100.
- Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.
- Ellison, P. T. 1994. Advances in human reproductive ecology. *Annual Review of Anthropology*, **23**, 255–275.
- Engels, F. 1884. *The Origin of the Family, Private Property and the State*. London: Penguin.
- Euler, H. A. & Weitzel, B. 1996. Discriminative grandparental solicitude as reproductive strategy. *Human Nature*, **7**, 39–59.
- Gabler, S. & Volland, E. 1994. The fitness of twinning. *Human Biology*, **66**, 699–713.
- Gaulin, S. J. C., McBurney, D. H. & Brakeman-Wartell, S. L. 1997. Matrilineal biases in the investment of aunts and uncles: a consequence and measure of paternity uncertainty. *Human Nature*, **8**, 139–151.
- Graham, W. 1991. Maternal mortality: levels, trends and data deficiencies. In: *Disease and Mortality in Sub-Saharan Africa* (Ed. by R. Feacham & D. Jamison), pp. 101–126. Oxford: Oxford University Press.
- Haig, D. 1999. Genetic conflicts of pregnancy and childhood. In: *Evolution in Health and Disease* (Ed. by S. C. Stearns), pp. 77–89. Oxford: Oxford University Press.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1–52.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology*, **12**, 12–45.
- Harpending, H. C. & Pennington, R. 1991. Age structure and sex-biased mortality among Herero Pastoralists. *Human Biology*, **63**, 329–353.
- Hawkes, K., O'Connell, J. F. & Blurton-Jones, N. G. 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long post-menopausal lifespans. *Current Anthropology*, **38**, 551–578.
- Hill, A. 1997. Truth lies in the eye of the beholder: the nature of evidence in demography and anthropology. In: *Anthropological Demography* (Ed. by D. Kertzer & T. Fricke), pp. 223–247. Chicago: University of Chicago Press.
- Hill, K. 1993. Life history theory and evolutionary anthropology. *Evolutionary Anthropology*, **2**, 78–88.
- Hill, K. & Hurtado, A. M. 1991. The evolution of reproductive senescence and menopause in human females. *Human Nature*, **2**, 315–350.
- Hill, K. & Hurtado, A. M. 1996. *Ache Life History: the Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter.
- Hobcraft, J., McDonald, J. W. & Rutstein, S. 1983. Child-spacing effects in infant and early child mortality. *Population Index*, **49**, 585–618.
- Hoem, J. 1992. Social policy and recent fertility change in Sweden. *Population Development Review*, **16**, 735–748.
- Holden, C. & Mace, R. 1997. A phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology*, **69**, 605–628.
- Holden, C. & Mace, R. 1999. Sexual dimorphism in stature and women's work: a cross-cultural analysis. *American Journal of Physical Anthropology*, **110**, 27–45.
- Howell, N. 1979. *Demography of the Dobe area !Kung*. New York: Academic Press.
- Hubback, J. 1957. *Wives Who Went to College*. London: Heinemann.
- Irons, W. 1979. Cultural and biological success. In: *Evolutionary Biology and Human Social Behaviour: an Anthropological Perspective* (Ed. by N. Chagnon & W. Irons), pp. 257–272. North Scituate: Duxbury.
- Johansson, S. 1987. Status anxiety and demographic contraction of privileged populations. *Population Development Review*, **13**, 439–470.
- Josephson, S. C. 1993. Status, reproductive success and marrying polygynously. *Ethology and Sociobiology*, **14**, 391–396.
- Kaplan, H. 1996. A theory of fertility and parental investment in traditional and modern human societies. *Yearbook of Physical Anthropology*, **39**, 91–135.
- Kaplan, H., Lancaster, J., Bock, J. A. & Johnson, S. E. 1995. Does observed fertility maximise fitness among New Mexican men? A test of an optimality model and a new theory of parental investment in the embodied capital of offspring. *Human Nature*, **6**, 325–360.
- Kirkwood, T. B. L. & Rose, M. R. 1991. Evolution of senescence: late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society of London, Series B*, **332**, 15–24.

- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- LeGrand, T. & Phillips, J. F. 1996. The effect of fertility reductions on infant and child mortality: evidence from Matlab in rural Bangladesh. *Population Studies*, **50**, 51–68.
- Loudon, I. 1992. *Death in Childbirth: an International Study of Maternal Care and Maternal Mortality 1800–1950*. Oxford: Clarendon Press.
- Low, B. S. 1991. Reproductive life in 19th century Sweden: an evolutionary perspective on demographic phenomena. *Ethology and Sociobiology*, **12**, 411–448.
- Lummaa, V., Haukioja, E., Lemmetynin, R. & Pikkola, M. 1998. Natural selection on human twinning. *Nature*, **394**, 533–534.
- Lund, E. 1990. Pattern of childbearing and mortality in married women: a national prospective study from Norway. *Journal of Epidemiology and Community Health*, **44**, 237–240.
- Mace, R. 1996a. Biased parental investment and reproductive success in Gabbra pastoralists. *Behavioral Ecology and Sociobiology*, **38**, 75–81.
- Mace, R. 1996b. When to have another baby: a dynamic model of reproductive decision-making and evidence from Gabbra pastoralists. *Ethology and Sociobiology*, **17**, 263–274.
- Mace, R. 1998. The co-evolution of human fertility and wealth inheritance. *Philosophical Transactions of the Royal Society of London, Series B*, **353**, 389–397.
- Mace, R. In press. An adaptive model of human reproductive rate with wealth inheritance: why people have small families. In: *Human Behaviour and Adaptation: an Anthropological Perspective* (Ed. by L. Cronk, W. Irons & N. Chagnon). New York: Aldine de Gruyter.
- Mace, R. & Holden, C. 1999. Evolutionary ecology and cross-cultural comparison: the case of matrilineality in sub-Saharan Africa. In: *Comparative Primate Socioecology* (Ed. by P. C. Lee), pp. 387–405. Cambridge: Cambridge University Press.
- Mace, R. & Sear, R. 1996. Maternal mortality in a Kenyan, pastoralist population. *International Journal of Gynecology and Obstetrics*, **74**, 137–141.
- Mace, R. & Sear, R. 1997. The birth interval and the sex of children: evidence from a traditional African population. *Journal of Biosocial Science*, **29**, 499–507.
- Moore, S. E., Cole, T., Poskitt, E., Sonko, B., Whitehead, R., McGregor, I. & Prentice, A. M. 1997. Season of birth predicts mortality in rural Gambia. *Nature*, **388**, 434.
- Nath, D. C. & Land, K. C. 1994. Sex preferences and third birth intervals in a traditional Indian society. *Journal of Biosocial Science*, **26**, 95–106.
- Pagel, M. D. & Harvey, P. H. 1989. Taxonomic differences in the scaling of brain weight on body weight among mammals. *Science*, **244**, 1589–1593.
- Pennington, R. 1992. Did food increase fertility? Evaluation of !Kung and Herero history. *Human Biology*, **64**, 497–521.
- Perls, T. T., Alpert, L. & Fretts, R. C. 1997. Middle-aged mothers live longer. *Nature*, **389**, 133.
- Perreira, M. & Fairbanks, L. A. 1991. *Juvenile Primates*. New York: Oxford University Press.
- Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. London: Chapman & Hall.
- Rogers, A. R. 1993. Why menopause? *Evolutionary Ecology*, **7**, 406–420.
- Scheper-Hughes, N. 1992. *Death without Weeping: the Violence of Everyday Life in Brazil*. Berkeley: University of California Press.
- Schneider, D. M. & Gough, K. 1961. *Matrilineal Kinship*. Berkeley: University of California Press.
- Seielstad, M. T., Minch, E. & Cavalli-Sforza, L. L. 1998. Genetic evidence for higher female migration rate in humans. *Nature Genetics*, **20**, 278–288.
- Shanley, D. 1999. Resources, reproduction and senescence: evolutionary optimality models. Ph.D. thesis, University of Manchester.
- Simoons, F. J. 1978. The geographic hypothesis and lactose malabsorption: a weighing of the evidence. *American Journal of Digestive Diseases*, **23**, 963–980.
- Skinner, W. 1997. Family systems and demographic processes. In: *Anthropological Demography* (Ed. by D. Kertzer & T. Fricke), pp. 53–95. Chicago: University of Chicago Press.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stearns, S. C. & Koella, J. 1986. The evolution of phenotypic plasticity in life history traits: predictions for norms of reaction for age- and size-at-maturity. *Evolution*, **40**, 893–913.
- Strassman, B. & Dunbar, R. I. M. 1999. Human evolution and disease: putting the Stone Age in perspective. In: *Evolution in Health and Disease* (Ed. by S. C. Stearns), pp. 91–101. Oxford: Oxford University Press.
- Symons, D. 1979. *The Evolution of Human Sexuality*. Oxford: Oxford University Press.
- Tracer, D. 1991. Fertility related changes in maternal body composition among the Au of Papua New Guinea. *American Journal of Physical Anthropology*, **85**, 393–406.
- Volland, E. 1988. Differential infant and child mortality in evolutionary perspective: data from late 17th to 19th century Ostfriesland (Germany). In: *Human Reproductive Behaviour: a Darwinian Perspective* (Ed. by L. Betzig, M. Borgerhoff-Mulder & P. Turke), pp. 253–262. Cambridge: Cambridge University Press.
- Weaver, L. T. & Beckerleg, S. 1993. Is health a sustainable state? A village study in The Gambia. *Lancet*, **341**, 1327–1331.
- Westendorp, R. & Kirkwood, T. B. L. 1998. Human longevity at the cost of reproductive success. *Nature*, **396**, 743–746.
- Williams, G. C. 1957. Pleiotrophy, natural selection and the evolution of senescence. *Evolution*, **11**, 398–411.
- Wood, J. W. 1994. *Dynamics of Human Reproduction: Biology, Biometry, Demography*. New York: Aldine de Gruyter.