6 Some current ideas about the evolution of the human life history

NICHOLAS BLURTON JONES, KRISTEN HAWKES AND
JAMES F. O'CONNELL

Introduction

Adolph Schultz's famous diagram (Fig. 6.1) aged well: human life history is characterised by a long juvenile period (weaning to reproductive maturity), and a long post-reproductive lifespan in females. Table 6.1 compares human and great ape life history parameters and invariants of Charnov (1993). Notable here are low adult mortality, high fertility squeezed into a reproductive span similar in length to that of *Pan* (thus, shorter interbirth intervals), late age at first reproduction and great length of the juvenile period.

How do we explain these differences between our nearest relatives and ourselves? This chapter summarises some recent attempts to use life history models on data from contemporary hunter–gatherers, and other non-contracepting populations with little access to modern medicine (see also Borgerhoff Mulder, 1991; Hill, 1993; and for a comprehensive review of hunter–gatherer research, Kelley, 1995).

Trade-off between numbers and care of offspring

Hill and Hurtado (1996) examine interbirth interval and the trade-off between increased fertility and increased infant and child mortality among Ache foragers in Paraguay. As in other populations, after controlling for early death of a previous infant, mother's age, and mother's weight, shorter interbirth intervals are accompanied by higher infant and child mortality. But, in contrast to Blurton Jones (1986; for discussion of Harpending's (1994) critiques see Blurton Jones, 1994; for Hill and Hurtado's results, see Blurton Jones, 1996), they found that this effect was much too weak to render the observed intervals optimal. Ache values predict that the optimal interbirth interval would be much shorter than is observed. Hill and Hurtado discuss possible reasons, suggesting that there must be costs to
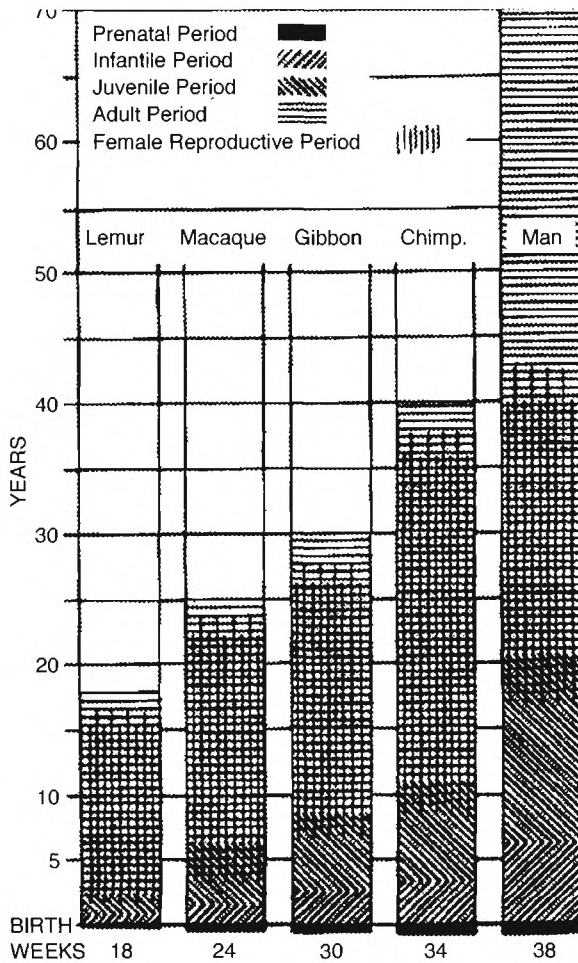
Fig. 6.1   Schultz's diagram of primate life histories. (Modified from Schultz, 1969.)

very short intervals that we have yet to appreciate. They also emphasise the effect of mother's size, bringing the study of human fertility closer both to the concept of productivity in Charnov's life history model and to primate literature (e.g. Lee, Majluf and Gordon, 1991; Lee and Bowman, 1995). But the source of Blurton Jones and Sibly's (1978) predictions (tested by Blurton Jones, 1986, 1987), maternal provisioning of juveniles, which so markedly distinguishes humans from other primates, will come back into the picture below.

Table 6.1. *Average values for selected life history variables*

	Average adult life span (years) ELC method (1/M)	Age at maturity[b] (years)	Age at weaning[c] (years)	α[d] (years)	αM	Weaning weight/adult weight[e]	Daughters/year[f]	αb
Orangutan	17.9	14.3	6.0	8.3	0.46	0.28	0.06	0.52
Gorilla	13.9	9.3	3.0	6.3	0.45	0.21	0.126	0.79
Chimpanzee	17.9	13.0	4.8	8.2	0.46	0.27	0.087	0.70
Human	32.9	17.3	2.8	14.5	0.44	0.21	0.142	2.05

[a]The method described in Charnov (1993, caption to Figure 5.6, p. 104) is used to estimate average adult life span (1/M) from maximum observed life spans (T_{max}): $1/M = 0.4T_{max} - 0.1$. Values for orangutans: Leighton *et al.* (1995); gorillas: Stewart, Harcourt and Watts (1988); chimpanzees: Nishida, Takasaki and Takahata (1990). The human value is estimated from Howell's (1979) oldest observed !Kung individual (age 88), and Hill and Hurtado's (1996) oldest observed (forest living) Ache individual (age 77).

[b]Age at first birth minus gestation. Orangutans: Leighton *et al.* (1995); gorillas: Stewart *et al.* (1988); chimpanzees: mean of means from Wallis (1997) for Gombe, Nishida *et al.* (1990) for Mahale, and Sugiyama (1984) for Bossou; humans: mean of the mode for !Kung in Howell (1979) and Ache in Hill and Hurtado (1996).

[c]Orangutans: Galdikas and Wood (1990); gorillas: Stewart *et al.* (1988); chimpanzees: the mean of the estimate from Goodall (1986) for Gombe and from Nishida *et al.* (1990) for Mahale; humans: the mean of the median for !Kung in Howell (1979) and Ache in Hill and Hurtado (1996).

[d]Defined as the period of independent growth, from weaning to maturity.

[e]Data from Lee *et al.* (1991) for the great apes. Maternal size for orangutans is estimated to be 40 kg, gorillas 93 kg, chimpanzees 40 kg. In that data set, δ for humans is 0.16 with maternal size at 55 kg (the upper end of the range for modern foragers who are generally smaller than contemporary non-foragers and pre-Mesolithic moderns). The mean of the !Kung (Howell, 1979) – who are at the lower end of the size range for modern foragers – and the Ache (Hill and Hurtado, 1996) – who are at the upper end – is used to represent humans.

[f]Great ape data from Galdikas and Wood (1990), who reappraise birth spacing in all species in the same way. Medians calculated therein (for closed intervals) plus two months are used to approximate the mean interval; then divide by 2 to get the rate for daughters. Galdikas and Wood use the Gainj, a population of horticulturalists in highland Papua New Guinea, to represent humans, for which $b = 0.132$. The mean of the !Kung (Howell, 1979) and the Ache (Hill and Hurtado, 1996) are used by the authors.

Belsky, Steinberg and Draper (1991) – taking their lead from Draper and Harpending (1982) and Pennington and Harpending (1988) – and Chisholm (1993) interpret variation in parental care and reproductive strategies in human societies as responses to high and uncontrollable mortality. Poverty and unpredictable environments were proposed to go with higher investment in fertility and less care, and earlier maturation, resulting from an early developmental shift triggered by parental care as an indicator of future reproductive opportunities. Empirical studies provide mixed support for earlier maturation among poorer or more stressed girls (e.g. Surbey, 1990).

Blurton Jones (1993) suggested that in humans parental fitness can be enhanced by effort allocated not only to numbers and survivorship of offspring but also to a variety of ways to enhance offsprings reproductive success, such as accumulating and endowing wealth and status, caring for grandchildren, teaching, arranging mates. Variation in returns to effort directed to such ends should predict variation in the amount of effort directed towards them. We might then be able to account for extensive variation in patterns of parental care. (The distinction between depreciable and non-depreciable care would play an important role in this enterprise.) For example, anthropologists have noted the scarcity of direct teaching – we would suggest that most mothers have more fitness-enhancing demands upon their time, such as housing and feeding themselves and their children. Where added effort directed towards shelter and food yields little increase in fitness, we expect to see parents taking more time to train and educate children. Kaplan (1996) developed a much more advanced model of the allocation of parental resources that links together issues as diverse as the demographic transition, education and health-seeking behaviour, socioeconomic status and labour markets, in what must be the most ambitious (and promising) invasion of the social sciences by evolutionary thinking yet undertaken.

Age at first birth

Hill and Hurtado (1996) report their intensive investigation of demography of the Ache hunter-gatherers of Paraguay by means of carefully interlinked interviews conducted between 1977 and 1995. The information covers a 'pre-contact' or 'forest' period, which ended in 1971, a brief but decimating (from 544 in 1970 to 338 in 1976) period of epidemics during the first years of settlement, and a subsequent period during which most people spent

most of their time at settlements, and the population rapidly grew to pre-contact levels – 537 people in 1989.

Hill and Hurtado examined women's weight as a predictor of fertility. After controlling for age, and whether the previously born child was dead or alive, they found a significant contribution of body weight to predicting time to the next birth. Heavier women had children after a shorter interval than lighter women. Thus, delaying maturation to grow bigger yields greater fertility. Delaying too long cuts into the time available to reproduce, and lowers the probability of surviving from birth until reproduction begins. Fitting real-life parameters to equations summarising this trade-off predicts an optimal age and weight at first birth. The observed Ache age at first birth (17.5 years) fits well with the prediction, but the model predicts maturity at greater weight than observed. Hill and Hurtado then fit !Kung weight and mortality data from Howell (1979) (but use the Ache regression of fertility on weight) to the equations and show that observed age at first birth fits the slightly higher age predicted (19 years). Growth data predicted the much younger age at menarche observed in the USA. Analyses of individual variation among fast-growing and slow-growing Ache girls provide further support for the generality of the model. Faster-growing Ache girls have their first baby earlier than slow-growing girls. Apparently, neuroendocrine maturation mechanisms do their job flexibly and efficiently.

Hill and Hurtado point out that variation in adult mortality rates within humans makes little difference to the calculated optimal age at maturity, but that lowering mortality to chimpanzee levels predicts maturity at 14 years – close to the 13 years noted in Table 6.1.

Like Stearns and Koella (1986), Hill and Hurtado sought the strategy that maximised fitness, measured as r (intrinsic rate of increase). Stearns (1992: p. 148) points out that Kozlowski and Wiegert (1987) examined maximisation of $\Sigma l_x m_x$ and obtained the prediction that faster growth predicted later maturity. This point, apparently commonplace to life history theorists, is noted as a warning to us 'end-users' that the field is complex, in flux, and there is as yet no single 'right' model.

Hill and Hurtado make an interesting excursion into male life histories: among Ache men who have completed their growth, fertility relates to size but follows an inverted U shape. They suggest that this is because very heavy men have lower hunting success than men of intermediate weight (their Fig. 11.12 is reminiscent of Lee's (1979) observation that taller !Kung had lower hunting success than shorter men). Using male mortality, growth rate, and age-specific and weight-specific fertility, Hill and Hurtado sought the optimal age at cessation of growth. The result shows that

optimal male age and size at cessation of growth are greater than for females, as observed among Ache and almost every other population. The model predicts body weight dimorphism ratio (male/female) of 1.03, rather than the observed 1.11. Hill and Hurtado draw several interesting further implications, for example that variance in body weight should be lower for men than for women, and among Ache it is.

They link these observations of developing hunting success to the idea that humans mature late because this allows them more time to acquire fitness-enhancing skills (Lancaster and Lancaster, 1983; Bogin, 1990; Lancaster, 1997). Kaplan's interest in human capital theory (1994), often used to discuss the costs and benefits of staying on at school, may lead to a more explicit version of this view. These authors have argued in another direction (Blurton Jones, Hawkes and O'Connell, 1997; Hawkes, O'Connell and Blurton Jones, 1997) and do so below.

Zero population growth?

Hill and Hurtado make a suggestion that runs counter to much that has been believed about human population dynamics. The zero population growth observed among the !Kung, and the density-dependent effects shown by Wood and Smouse (1982) for the Gainj were taken to confirm that in prehistoric times our species conformed to the expectable steady state, density-dependently controlled, level population size. Population growth would thus result slowly from expansion into new habitats, and from technological advances. Our currently high rates of population growth were then regarded as some errant outcome of modernity arriving in the Third World.

Hill and Hurtado point out that the accumulated data suggest otherwise. Mortality levels (especially adult mortality) in populations without access to modern medicine (they list Ache, Batak, Yanomamo, !Kung, and the authors would add Hadza – Blurton Jones *et al.*, 1992) are high by modern standards but are very low compared to our primate relatives, including other great apes. Human fertility also – whether you take the low-fertility !Kung (total fertility rate, TFR 4.7: Howell, 1979; or 5.05; Blurton Jones, 1994) or the high-fertility Ache (TFR 8.3) or the intermediate Hadza (TFR 6.2) – is high by the standards of our nearest relatives (as shown in Table 6.1). These figures suggest extremely rapid rates of increase, as are actually displayed by the Ache and the Hadza. Hill and Hurtado suggest that a saw-tooth pattern may have characterised much of human evolutionary history. !Kung zero population growth may owe its

existence to sexually transmitted diseases of the reproductive tract (STDs) that greatly increased in frequency with the arrival of larger numbers of herders in the 1950s (Harpending, 1994).

It may not be unusual to observe short-term imbalance of fertility and mortality in animal populations and we should be cautious about Hill and Hurtado's suggestion. But simulations suggest that the 400–1000-person forager populations can give reliable demographic data (Jenike, personal communication), so Hill and Hurtado's argument cannot be dismissed as due to unreliable data. Furthermore, Hill and Hurtado point out that fertility and mortality schedules are part of the coherent pattern that links life history parameters together. If our mortality schedule was 'really' chimp-like, there could have been no selection pressure to produce individuals that senesce so much later than chimps. Nor would humans be the size they are, nor mature at the age they do. Hill and Hurtado point out that 67% pre-adult mortality would be needed to give a constant population with a 48-month interbirth interval (the upper extreme observed among foragers; shorter interbirth intervals require even higher mortality), and comment 'Such high mortality has never been observed in any traditional population'.

Thus, Hill and Hurtado imply that a long-standing feature of human biology may have been not just the Malthusian possibility, but actual rapid increase, and a saw-tooth population history. They suggest that this may influence our ability to assess accurately the significant selective forces responsible for our biology and behaviour: 'Perhaps trade-offs were not detected, and menopause not favored by kin selection, because the Ache were in a period of resource abundance'. There must also be implications for archaeologists' ideas about invention and 'intensification' as a response to population pressure.

Helpers

Humans are expert at recruiting and distributing help. Hill and Hurtado suggest that many costs and benefits of alternative ways of behaving, growing and reproducing may be rendered unmeasurable by the ability of the individual who 'made an error' to cover it by recruiting help from kin, who also benefit from helping to remedy the miscalculation. Thus, a grandmother gains more fitness by going to go to help her daughter who bore too many children too fast (and thus risks being unable to feed them) than to her daughter who has few (depending on why the latter has few!). Grandmother's decision then reduces the effect of her daughter's 'miscalculation'. If instead the first daughter has more children because she

already has helpers and better circumstances, it may pay the mother to go to help the second daughter, if her slow reproduction is due to lack of help or other soluble hardship. But it also follows that individuals who can recruit more help have different optima from those with no helpers. A woman who has a co-resident mother and a co-resident childless aunt can well afford to bear babies faster than her orphan friend.

Despite Turke's (1988) early work on daughters (see also Blurton Jones *et al.*, 1997), the study of men and grandmothers as 'helpers' has dominated recent work. Hawkes (1990, 1991, 1993) has argued against the widely held view that hunting is best understood as paternal investment, and that this was the major force in human evolution. We will continue to investigate hunting less as 'bringing home the bacon' and more as acquiring and distributing political 'pork'. An even more uniquely human class, that of grandmothers, has attracted more attention.

Hill and Hurtado (1991, 1996: p. 433) tested the classic version of the grandmother hypothesis of menopause: do the benefits of help given to daughters outweigh the benefits of continued child bearing? Ache demographic values show that, even under the most favourable assumptions, the effect of help on kin would have to be massively increased to give menopause a selective advantage. Ache women provide only 13% of the calorie income, and Hill and Hurtado note that the analysis needs to be repeated in populations in which women's contribution is much greater. Nonetheless, Hill and Hurtado (and Rogers, 1993) show that the effect would have to be almost unrealistically large.

Appealing to Schultz (Fig. 6.1) for initial support, Hawkes *et al.* (1997) have suggested that the derived character awaiting an explanation is post-reproductive life, not 'early cessation of fertility'. Chimpanzees cease to reproduce by 40, and their somatic senescence coincides with this. Human females cease to reproduce at about the same age but remain active and strong, and survive, even without access to modern medicine, for many years after this – women's life expectancy at 45 is 22 years for Ache (see Table 6.1 in Hill and Hurtado, 1996), 19.9 years for !Kung, and 21.3 years for Hadza (Howell, 1979; Blurton Jones *et al.*, 1992, from best fitting stable population models in Coale and Demeny, (1983) – but is close to zero for Gombe chimpanzees. The adaptation question then becomes: what could give rise to a selective advantage for delayed somatic senescence in an animal that is no longer reproducing? Natural selection cannot act on a post-reproductive individual unless there is a way in which its survival can influence the spread of its genes even after it has finished reproducing. Help given to descendants could have just this effect.

Hadza women past the childbearing years forage as efficiently as

Table 6.2. *Some return rates for human foragers*

Species	Part	Users	kcal/h on site	kcal/h with travel	kcal/h by child on site[c]	Daily yield[a] 7-hour day	People fed at 2000 kcal/day[d]
Adansonia digitata	Fruit	Hadza	1745–2328	1745–2328	600	12 215–16 296	6.1–8.1
Ricinodendron rautanenii	Nut	!Kung	2325–2738	727 +		5089–7000	2.5–3.5
Vigna frutescens	Tuber	Hadza	1615–1955	1423–1723	200	9964–12 062	4.98–6.03
Grewia retinervis	Berry	!Kung	187–973	113–335		791–2345 (1353–4024/ 12-hr day)	0–1
Grewia bicolor	Berry	Hadza	497–1130				
Cordia gharaf (undushi)[b]	Berry	Hadza	2771		2223		
Salvadora persica (tafabe)[b]	Berry	Hadza	1281		964		
Coccinea rehmannii (Tan)	Root	!Kung	2886	?	?	?	
Vigna dinteri (Sha)	Root	!Kung	3043	?	?	?	
Eminia antenullifera (makalita)	Tuber	Hadza		2000	500	14 000	7
Panjuko	Root	Hadza		1600	500	11 200	5.6

The authors sought two kinds of information, mostly from data presented in Hawkes *et al.* (1989, 1995, 1997) and in Blurton Jones *et al.* (1989, 1994b, 1997). (1) Return rate on encounter: if an individual encounters a food plant or patch, how many kcal does it get per minute of picking, digging or whatever it takes to acquire the resource? For some of the foods that humans target, processing costs are small (e.g. some roots). For others (Baobab fruit, Mongongo nuts), processing costs are high. These were reported where available. (2) Estimated returns per day: some of the foods humans target are distributed through the environment in very localised patches; Mongongo nuts are an extreme example. Thus, the time people have to spend to get to the patch is an importnat issue, and it reduces the daily return rate considerably. These figures are quite approximate. They may only roughly bracket seasonal, annual and local variation.

[a]Day yield includes travel time, which is very large for *Ricinodendron*, and sometimes very large for *Cordia* and *Salvadora*.

[b]No data exist for other primates using these very high-return berries.

[c]Figures for human dietary requirements are widely used, and are believed to err on the generous side. The authors use a figure of 2000 kcal/day for an active forager-sized woman, and another 2000 for each child (suppose an assortment from 5 to 15 years old). They divide the daily return rates shown in Table 6.3, for a seven-hour day, by 2000 to find the number of people a woman could feed (including herself).

[d]Return rates for Hadza children picking undushi and tafabe berries are from Hawkes *et al.* (1995). The figures for Baobab, //ekwa, makalita and panjuko are those for a 10-year-old child, read from the plots of returns against age in Blurton Jones *et al.* (1997).

younger women, and work slightly longer hours, and so bring home more food (Hawkes, O'Connell and Blurton Jones, 1989). Hawkes *et al.* (1997) show that the growth of weaned children of women with a suckling infant correlates with their grandmother's work hours, not with their mother's. Thus, older women's foraging may increase the fitness of their young descendants.

The opportunity to help depends upon the use of highly productive resources that are difficult to acquire or process, such as tubers and nuts (Table 6.2). Hawkes *et al.* (1997) suggest: (a) that use of these resources both allows and gives rise to the need to provision juveniles, who can acquire or process them only inefficiently if at all (see Hawkes, O'Connell and Blurton Jones, 1995, and Blurton Jones *et al.*, 1994a and 1994b, for analyses of the variety of combinations of mother and juvenile foraging displayed by Hadza and !Kung); and (b) that the need to provision juveniles provides an opportunity for helpers to make a difference to the fitness of close relatives.

The main point about Hawkes *et al.*'s grandmother hypothesis is the interesting set of links to other life history parameters, which are now outlined. One of the most successful attempts to offer a unified theory of life histories is that of Charnov (1993) – CM. CM shows that relationships among certain variables remain approximately 'invariant' across wide ranges in body size. These relationships account for the correlations long recognised among life history variables and body size, and also for correlations among life history variables when body size is removed. Primates, for example, have 'slow' life histories compared with other mammals of similar size (Harvey, Promislow and Read, 1989). This can be explained as a result of a difference in the 'production function' for primates.

CM assumes that 'production' can be allocated either to growing oneself or to growing offspring (Charnov, 1991, 1993; Charnov and Berrigan, 1993). This simple model divides growth into two periods: (1) conception to weaning, in which growth is set by the mother's production (a function of her size); and (2) weaning to maturity (α), in which growth is a function of an individual's own body size. At maturity, production previously allocated to growth is redirected to babies. Growth rates are a function of body mass (W), a characteristic 'production coefficient' (A), and an allometric exponent (c). Individual growth rates take the form: $dW/dt = AW^c$, where production energy at time t for an individual of body mass W equals the production coefficient times body mass to the c power (usually assumed to be 0.75). Adult size for a given period of independent growth (α) and the production available to funnel into offspring for a given adult size both depend on A. If A is large, the result is faster growth and production (for a given size) to funnel into babies. Primates have a very low A, averaging less

than half that of other mammals. This accounts for small size at a given age of maturity and low fecundity for size compared with other mammals (Charnov and Berrigan, 1991, 1993).

CM assumes that, given adult life span, selection sets the evolutionarily stable strategy for duration of independent growth (α) according to the trade-off between (1) the benefits of growing longer, and so being larger with more production to put into offspring, and (2) beginning to reproduce sooner, and so having a greater chance to reproduce before dying. CM assumes that key features of the mortality schedule can be modelled as an early burst of high mortality followed by a drop to adult mortality levels before age of first reproduction. Because production put into babies is a function of maternal size (W_α), that production increases with age of maturity. The time available to use those gains depends on adult life span, the inverse of the instantaneous mortality rate (M). As adult life span increases (adult mortality rate falls), selection favours delayed maturity to reap the gains of larger size. Thus, both a and M vary widely but inversely. Their product (αM) is approximately invariant.

There is another constraint in this model: the size at which babies are weaned is a function of adult body size. For a sample of mammals (and for primates separately), the ratio of size at independence (weaning) to adult size ($W_o/W_\alpha = \delta$) is approximately constant (Lee *et al.*, 1991; Charnov, 1993). Because δ scales almost isometrically with body size while production scales up more slowly (the growth allometry is a power of 0.75), the size of weanlings goes up faster with maternal size than does the production the mother can put into them. Thus, annual fecundity, the number of daughters produced per year (b), goes down as age at maturity (α) goes up. Larger mothers produce larger but fewer babies, making αb another approximate invariant.

These 'assembly rules' for mammalian life histories seem quite robust. The general fit of empirical patterns to the predictions of CM (since confirmed on other, larger data sets: Purvis and Harvey, 1995) suggests that the model identifies key trade-offs that shape mammalian life histories. The invariant relationships reveal scaling rules: some life history variables are adjusted to others. In this model, fecundity depends on age at maturity, and age at maturity is adjusted to adult life spans. If ancestral human life spans increased due to grandmothering, then that increase should have distinctive effects on the age at maturity, time or size at weaning, and fertility.

Grandmothering, age at maturity, interbirth intervals, and fecundity

In CM, αM is approximately invariant because longer life spans favour more advanced age at maturity. More time to accrue the benefits of increased production associated with growing longer before reproducing offsets the cost of delay. If gains from growing longer continue to pay off *after* menopause, as the grandmother hypothesis proposes, then α should be adjusted accordingly. It is. These authors found that the late age at maturity for humans (high α) combined with our long life spans (low M) result in an αM similar to that of the other great apes. The delay in maturity for humans is as predicted if the gains from growing longer before reproducing pay off throughout adulthood, during *both* childbearing and grandmothering years.

If the grandmother hypothesis is correct, it also implies that childbearing women must be producing babies faster than otherwise expected because of grandmothers' contribution to that production. Human interbirth intervals *are* smaller than those of any other great ape (Galdikas and Wood, 1990). Grandmothers could affect the growth of infants in one of two ways: (1) they might contribute to nursing mothers directly, and so add to the production that goes through them to infants, who would then grow to the size of independence faster than otherwise expected; or (2) mothers might wean infants before they reach the expected size of independence because they can pass the youngsters on to grandmothers, who supply the necessary nutrient stream.

The second alternative is suggested by the contribution grandmothers make to the nutrition of their weaned grandchildren (Hawkes *et al.*, 1997). In the light of the Hadza pattern, the authors hypothesised that grandmothers allow mothers to wean infants earlier than they otherwise might. If so, weaning would mark a shift to grandmother's support, not feeding independence, and so δ (the ratio of weaning weight to adult weight) would be lower for humans than for other apes.

The ratio of offspring size at weaning to maternal size ($W_o/W_\alpha = \delta$) is approximately 0.33 across the mammals generally, and primates in particular (Lee *et al.*, 1991; Charnov, 1993). All the great apes (Lee *et al.*, 1991) have δs lower than the order mean (see Table 6.1), which illustrates the slight negative relationship between δ and maternal size in both primates and other mammalian taxa (Lee *et al.*, 1991; Charnov, 1993; Purvis and Harvey, 1995). *Within* the apes there is no relationship between δ and adult body size. The authors used the mean of two ethnographic hunter–gatherer values (Ache: Hill and Hurtado, 1996; and !Kung: Howell, 1979) to rep-

resent δ for humans (see Table 6.1). That value is not lower than all the other great apes, although it ties with that of gorillas for lowest place, a result that is at best equivocal for our expectation that humans wean at a relatively small size.

It is possible that our estimate for human δ errs on the conservative side (i.e. against the hypothesis). There appears to be a much greater variation in adult than in weanling sizes in humans (Lee *et al.*, 1991), so a larger sample of human populations might dilute the large effect of the small size of !Kung adults in our sample. The δ value for humans in Lee *et al.* (1991), for which the sample is not restricted to foragers, *is* much lower than all the other apes (0.16 compared to 0.21 for gorillas, 0.27 for chimpanzees, 0.28 for orangutans). Ethnographically known hunter–gatherers are generally smaller than pre-Mesolithic human populations, so perhaps the δ for Paleolithic moderns was closer to the Lee *et al.* value.

Our short interbirth intervals, perhaps made possible by a small δ, are especially striking given the negative scaling of fecundity with age at maturity across the mammals. Because b (daughters per year) scales approximately with α, the direct comparison of interbirth intervals underestimates the relatively high fertility of humans. Later age at maturity is usually associated with reductions in b. But if later maturity in humans is due to grandmothering, then grandmothers' contribution to production will have important countervailing effects that *increase b*.

Across the primates and mammalian taxa generally (of all sizes), αb is approximately 1.7 (Charnov, 1993). For all the other great apes, the αb number is substantially lower than this, less than 1.0. Humans, however, have an αb value greater than than 2.0, more than double the other large-bodied apes. The grandmother hypothesis predicts just this: αb *should* be high because it incorporates the production of *both* mothers *and* grandmothers. The baby production of the entire life span is concentrated in the childbearing years.

The grandmother hypothesis combined with CM accounts for several distinctive features of human life history, including long life spans after menopause, late age at maturity, short interbirth intervals, and high fertility. Other hypotheses have been offered to explain each of these individually (Smith and Tompkins, 1995), but 'grandmothering' can explain them all at once.

Criticisms of the grandmother hypothesis

The grandmother hypothesis has attracted several critical comments, among them:

1. Old Hadza women help young kin, but is this a general pattern (Gibbons, 1997)? Hill and Hurtado (1991) show an effect of Ache grandmothers upon their daughters' reproduction, and !Kung informants of Blurton Jones, Hawkes and Draper (1994a) claimed that older women, less distractable and tougher, are the most productive foragers.

2. What about meat obtained by males, which often forms around 50% of the food intake in hunter–gatherer populations? CM implies that attention to female life histories is sufficient to account for major taxonomic variation. But as long as females can access the meat, it has an effect on female economics – the debate is not concluded!

3. Some chimpanzees use resources juveniles cannot process (Table 6.3), they sometimes give food to juveniles, and some live beyond their apparent reproductive span. Is grandmothering really distinctly human? Great ape populations are so small that meaningful comparative data take years to accumulate. The chimpanzee nut-cracking data are very important; they support the view that hard-to-process food is a context in which adults transfer food to juveniles. If nuts were the staple food of these populations, we might expect to see benefits to delayed senescence. But the nuts are used for only a third of the year, are not available in some years and, most intriguing, are only exploited for about an hour a day (Sugiyama and Koman, 1979a, 1979b; Boesch and Boesch, 1984).

4. Current evidence suggests patrilocality as a conservative hominoid trait (Foley and Lee, 1989). Would grandmothering work as well in patrilocal groups as in the matrilocal groups it has been studied in? The authors would rank grandmother's fitness benefit accruing from help to children of beneficiaries as: greatest from help to daughter > sister > niece > son > nephew because of relatedness and paternity uncertainty. (Grandmother as mate guard is a role we have not examined. It might have interestingly different implications for life history.) For grandmothering to win over continued births, the only hopeful candidate would be help to daughter; help to others is too heavily discounted. But help to any of these might be adequate to select for delayed senescence. Thus, the grandmother hypothesis could apply to either matrilocal or patrilocal settings. But grandmothers benefit most by living with their daughters and should favour matrilocality. Provisioning enables older juveniles to help their mother, offering another advantage to keeping daughters at home. (Blurton Jones *et al.*, 1997, suggest that teenage sons pursue interests that conflict with efficient provisioning of younger siblings.) If men gain by kin co-operation in hunting, or the defence of females, they should favour patrilocality.

Table 6.3. *Returns on food patches for primate species and human foragers, and an estimate of the number of individuals that could potentially be supported by a foraging individual*

Species	Resource	kcal/hour in patch	kcal/day	Expend/ day	Number that can be supported
Papio cynocephalus[a]	Various	297	1013	626	1.62
Cercopithecus aethiops[b]	Acacia flowers	311	1244	505	2.46
M. fuscata[c]	Seeds	115	717	529	1.36
Pan troglodytes[d]	Coula nuts	1408–1508	2616 (potential maximum 9856–10 556)	1767	1.48 5.6–5.97
Pan troglodytes[e]	Figs	1200	?	1767	?
Homo sapiens	Baobab fruit	1700	11 900	2400	4.96

[a]Baboons (Stacey, 1986): feeding efficiency seems to show 'on-site' returns of 20.7 kJ per min = 1242 kJ/h = 297 kcal/h. Stacey's 'foraging efficiency' includes moving during the day, which seems equivalent to the authors' foraging returns with travel time and processing included. Stacey gives 9.4 kJ/min (564 kJ/h), which is 135 kcals/h; multiply this by 7 hours' work = 945 kcal/day. Food intake is 385 kJ/kg per day (57 kcal). Females weigh 11 kg = 4235 kJ per female per day. Energy expenditure calculated at 238 kJ/kg per day. Females of 11 kg need 2618 kJ per day. Ratio of intake/expenditure = 1.51–1.62.

[b]Vervets: feeding returns = 311 kcal/h (Lee, personal communication), with 4-hour foraging day = 1244 kcal/day intake. Food requirement calculated as 2 × BMR, with 65% digestible energy. Vervet female weight = 3.15 kg; ratio of intake over requirements = 2.46 individuals (self plus 1.46 others).

[c]Japanese macaque (Saito, 1996): intake rate up to 8 kJ/min on seeds Zelkova and Carpinus = 480 kJ/h/4.18 = 115 kcal/h. Return rate × feeding time up to 3000 kJ/day = 717 kcal/day. Weight of female *M. fuscata* is 9.2 kg (Lee et al., 1991). Using Stacey's 238 kJ/kg per day expediture = 2189.6 kJ/day per female (or 529 kcal/day). A female *M. fuscata* can support 717/529 = 1.35 individuals (i.e. self and 0.35 more) on these berries. Assuming a 7-hour foraging day, 115 kcal/h × 7 = 805 kcal/day. This calculation suggests she can support 805/529 = 1.52 individuals.

[d]Chimpanzee (Boesch and Boesch, 1984): female weight is 31 kg = 1767 kcal/day expenditure. If we take Boesch's 'mean intake per individual and per day represents 2616 kcal', then a female chimp can only support 2616/1767 individuals = 1.48. But the 2616 kcal are obtained in only 1.5 h at an anvil site. This represents 1744 kcal/h. Other figures in Boesch suggest 1408–1508 kcal/h. These figures are comparable to human return rates. Not surprisingly, if a chimp stayed at the anvil for a 7-hour day, it could support more than five individuals.

[e]Chimpanzee (Wrangham et al., 1993): midpoint in plot of return rates in fig trees = 1200 kcal/h. If the supply was not depleted over 7-hours foraging, in one tree it could obtain 8400 kcal. 1767 kcals are required per day and 4.75 individuals could be supported in the tree.

The resulting conflict of interest should give the kind of variability Ember (1975) reports for human hunter–gatherers, and is in line with ideas about animal group transfer patterns (Greenwood, 1980; Pusey and Packer, 1995).

5. Isn't it too easy (cheating?) to give up assessing the trade-off between care for kin and another birth (even though evidence against it is accumulating), and switch attention to selection for delayed somatic senescence? We have long thought of menopause as a special adaptation, an endocrine modification that brings reproduction to an early end. But evidence for such a view is scant. The prime mover in menopause appears to be the loss of oocytes. Other mammals show a similar rapid loss of oocytes as they age. Experimental removal of ovarian tissue early in life hastens a later decline in reproductive rates (see Adams, 1984). Finch (1990) concludes his survey of the literature 'The oviprival syndromes of reproductive senescence seem to occur widely in mammals'. Given the high attrition rate of oocytes, extending the reproductive span may require prohibitively costly increases in investment in reproduction during prenatal development (Wood, 1994). Evidence compatible with such a trade-off between early investment and later reproduction is offered by Cresswell *et al.* (1997), who found in longitudinal data that early menopause was associated with indicators of retardation in the woman's own prenatal growth. A few mammals appear able to extend the reproductive span as long or longer than the human span: elephants, perhaps, and the long-finned pilot whale *Globicephala melaena* (Marsh and Kasuya, 1986), in contrast to the short-finned pilot whale (*G. macrorhynchus*) with 25% of adult females as post-reproductive. A selectionist examination of the peculiar development of the mammalian female germ line might be rewarding. If it can be interpreted as another manifestation of the contrast between male pay-offs from quantity and female pay-offs from quality (quantity being limited by gestation), then we must suppose repeated mitosis (found in sperm production throughout the individual male's life but in females contributing to oocyte production only before birth) poses a greater threat to quality than the suspended, resting state of the primary oocyte. Some data on mutation rates appear to support this suggestion (Drost and Lee, 1995).

6. Why would any animal take on the burden of provisioning juveniles? Are we not suggesting evolution into a disadvantage from which the animal is rescued only by the simultaneous, improbable and rapid arrival of grandmothers? Table 6.2 show s that staple foods used by !Kung and Hadza women allow them to provide for several dependents,

Table 6.4. *A South American example: plant foods of Ache and* Cebus apella

Species	Part	User	kcal/h
Arecastrum romanzolfianum	Growing shoot	Ache women	1584
	Fibre starch	Ache women	2246
	Fibre and shoot	Ache	2436
Casimiroa sinesis	Fruit	Ache	4181
Philodendron sellam	Unripe fruit	Ache	2708
	Ripe fruit	Ache	10078
Campomanesia zanthocarpa	Fruit	Ache	6417
Rheedia brasilense	Fruit	Ache	3245
Acromia totai	Nut	Ache	2243
Astrocaryum murumuru	Flower	*Cebus apella*	56.5
	Seeds	*C. apella*	191.3
Scheelia	Fruit	*C. apella*	127.2
	Frond pith	*C. apella*	63.4
Quararibea cordata	Nectar	*C. apella*	148.4
Strychnos asperula	Fruit	*C. apella*	174.2
Ficus kilipii	Fruit	*C. apella*	80.8

Ache plant foods from Table 2 in Hill *et al.* (1987; fruits for which $n < 10$ excluded). *Cebus apella* from Table 1 in Janson (1985). Return rates for Ache children are currently not available. The preponderance of fruit is discussed in the text. Nuts and palm parts require processing to render them accessible.

and that juveniles exploit these resources only inefficiently. Table 6.3 suggests that, with the important exception of chimpanzees, other primates acquire resources at a rate that does not generate a surplus. Thus, exploiting tubers and nuts, even though they must be provided for juveniles, appears likely to at least match the alternative strategy.

Table 6.4 offers a South American example and an important puzzle. This table compares plant foods of Ache foragers – forest dwellers among whom women acquire only 17% of the calories, in contrast to !Kung (58%) and Hadza (about 50%) – and *Cebus apella*. Notable here are the absence of tubers and the presence of just one nut in the Ache diet. Yet, the return rates Ache derive from fruit far exceed those of *Cebus*. Skill and agility seem unlikely to account for this difference. More likely candidates may be found in body size, gut transit times, or in the possession of baskets in which to stash fruit instead of waiting until the previous mouthful has been chewed. The low kcal/h return rate of primate foraging may result from a limit to the speed at which food can be processed, not a limit to the rate at which it could be acquired. Thus, it might be that many primates could acquire food fast enough (if

they were going to give it away and thus avoid their lengthy preprocessing) to produce a surplus and provision offspring. But the chimpanzee data, which suggest this most strongly, are in-patch acquisition rates, which leave us ignorant about how much of the day these rates could be sustained, and how much of the year. Important aspects of the rich but hard-to-acquire resources used by humans may be that their total biomass is very great, their seasons very long, and because they are difficult and time consuming to extract, competition takes the form of comparative skill and strength at extraction more than immediate interindividual competition for access, and hence depletion is slower. These considerations emphasise the role of juvenile inefficiency in the evolution of provisioning and show that the grandmother hypothesis may guide forager researchers towards greater participation in comparative research on primate and hominid diets.

7. Does provisioning juveniles really give a greater opportunity for helpers to enhance their fitness? Could helpers not help any primate mother just as much? Non-human primates provisioned in captivity maintain interbirth intervals half as long as in the wild. Any mammalian mother could gain from a helper, but helpers are found mostly among carnivores (including non-reproducing but not post-reproductive helpers) and humans. As suggested above, perhaps not all mammals can produce a surplus. But we also questioned this interpretation of the foraging data, and another argument may be considered. If we look at potential losses of fitness when the mother is temporarily incapacitated, the provisioning mother (who lives in an ecology in which her juvenile offspring cannot efficiently forage for themselves) appears at risk of losing the products of great portions of her reproductive career (dependent juveniles), while the non-provisioner appears at risk of losing only the current infant, or a delay to the next birth. Thus, the long-term contribution of a helper may be much greater when there is a series of still-dependent weaned offspring.

8. Is it right to divorce the evolution of human life history from the evolution of a large brain? Many authors have attempted to link the advantages of learning to large brains, and particularly to late maturity (Bjorklund, 1997, is a recent and unusually thorough example). Childhood is seen as a time for learning; more time spent learning improves adult competitive ability and the delay is repaid. Blurton Jones *et al.* (1997) suggested juvenile life is primarily waiting time, which could be filled with fitness-enhancing activities such as learning, if not too costly. Let us continue our devil's advocacy. Individuals who acquire skills

more rapidly are presumably at an advantage over those who acquire them slowly – they benefit from the skills without losing by delayed reproduction. Thus, a skill-based subsistence should select strongly for rapid learning (and the rapid construction of a brain that performs such rapid learning – most brain growth is accomplished within the first five years of life, why then would having a large brain account for another 12 pre-reproductive years?). If the length of life span renders cultural transmission useful (Boyd and Richerson, 1985, show cultural transmission is most useful at intermediate rates of environmental change; rate is relative to generation time), there may be an increased pay-off to rapid forms of learning. (We would draw the causal arrows from longer adult span, to late maturity, to long generation time, to increased pay-off from cultural transmission, to advantages in observational and 'hearsay' learning, to increased brain size.) Even if we concede that there is 'lots to learn' to be a successful forager, it is easier for us to believe that this selected for faster mechanisms of learning (such as observational learning) than that it selected for later maturity. A selective advantage to faster learning, employing mechanisms of learning not widely found in other species, seems more likely to account for the evolution of a large brain than does an assumption that because there is so much to learn we need to take longer to learn it. There seems to be ample experimental evidence that mechanisms of learning seen in other species would, indeed, require a long time (many trials) to acquire many skills and much cultural or topographical knowledge. 'Skill theory' proponents need to decide whether they wish to explain big brains or late maturity! If humans were acquiring more knowledge with a monkey's brain, it would indeed take many years to learn what young foragers know! But what we see among hunter–gatherers are individuals with the capacity to observe an older individual prepare a skin, cut climbing pegs, winnow Baobab flour, perform sacred dance steps, etc., and immediately repeat the activity themselves. These authors suggest that the human brain, while in a sense just more of the same, is not providing merely more space to store more information, nor merely more of the same learning mechanisms, but rather exhibits processes weakly evidenced in other species but startlingly efficient in our species.

If causal arrows are to be drawn from Machiavellian learning to big brains, and (separately, because brain volume reaches close to adult levels long before maturity) to late maturity, we need to spell out the components of Machiavellian intelligence that can be added with a larger brain and are absent from other primates, and we need to show whether these things take a long time to learn. Because many aspects of

social interaction must be shaped by real interests and power differences (including size and weaponry, and the interests of allies), it is likely that the scheduling of development of juvenile social intelligence is not determined by difficulty or time needed to learn but by the need to keep out of unnecessary trouble.

9. If grandmothering is such a good idea, why do we not see menopause or post-reproductive life in more species? Vervet grandmothers contribute to the fitness of their daughters and granddaughters (Fairbanks, 1988) but reproduce until death. If it is not costly to produce enough oocytes to last five or ten years, the trade-off that we should consider for the vervet may be between help to kin, and continued births (the 'classic' trade-off examined by Hill and Hurtado, 1991, and Rogers, 1993). This is even less likely to pay when: (a) the help given is non-depreciable, thus less impaired by the addition of offspring, and (b) the grandmother has already transferred some of her status to her daughters, in which case the marginal difference made by the grandmother is unlikely to out-weigh the benefit to her of continued reproduction.

We should ask a parallel question about Belsky *et al.* (1991) and Chisholm's (1993) view of differences in parental strategy, and perhaps even of Kaplan's (1994) view of demographic transition: why do high-ranking primates not have fewer offspring than low-ranking ones? The distinction between depreciable and non-depreciable care is critical here, too. Kaplan (1996) attends to highly depreciable care – money, direct instruction, social–intellectual interaction – that improves the child's chances in the competitive labour market. The nearest analogy in other animals is rank order, but its maintenance is non-depreciable. High-ranking vervets gain nothing by distributing this care among fewer offspring.

Discussion and conclusions

This chapter concentrates on efforts to apply perspectives from life history theory in biology to data on contemporary hunters and gatherers. Topics include the allocation of resources between offspring number and fitness, age at first reproduction, lack of balance of fertility and mortality schedules, the special significance of helpers in human adaptation, and contrasting ideas about the evolution of post-reproductive life. These investigations share an interest in ecological contexts that may have shaped the life history parameters. Each attaches primary importance to rich resources that are difficult for juveniles to acquire (meat, deep roots

and difficult nuts). The significance of such foods has been frequently discussed (e.g. Hatley and Kappelman, 1980). There are disagreements about the relative importance of hunting and the exploitation of difficult-to-acquire but rewarding plant foods, and about the way in which the development of the ability to exploit either resource accounts for the human life history.

The opportunities for meaningful comparisons of humans and other primates are greatly increased by the addition of more quantitative studies of hunters and gatherers. The Ache and Hadza studies add significantly to the landmark studies of the !Kung San, showing us both variability and commonality. Quantitative study of the use of plant foods (and hunting methods) among farmers and pastoralists would also provide useful information for comparative and evolutionary debate. More long-term studies of primate demography would also be very useful.

From the Hadza and San studies (e.g. Lee, 1979), we are beginning to build knowledge of African savanna economics to add to the comparative studies of Peters and O'Brien (1981), Peters (1987) and McGrew, Baldwin and Tutin (1988). Despite the obvious relevance of understanding savanna foraging ecology to the rational discussion of human origins, many data have yet to be collected. We need more data on the returns obtainable from such foods in different savanna habitats (enough traditional use of wild plants persists for useful work to be done), and the assumed association of roots and nuts with savanna habitats needs testing by quantitative analysis of availability in different kinds of forest (Vincent, 1985; Peters, 1987; McGrew *et al.*, 1988). Foraging return data from Hadza and !Kung and other users of wild plants can suggest which plants critically define forager habitats. Data on primate foraging that are easier to reconcile with foraging theory would be very useful. The authors were surprised by the difficulty of finding and comparing foraging data from primates. Comparative rainfall data for chimp habitats are made usefully available by Moore (1992). At 1717 mm/year, the mean rainfall is about five times (and even the driest localities are some three times) the rainfall in !Kung and Hadza country. Foley (1982) showed that prehistoric hunters and gatherers probably occupied areas with rainfall and productivity higher than the habitats of contemporary foragers. But we do not know the consequences of such differences for the real-life economic decisions of foragers. Peters' (1987) maps suggest that productive, hard-to-exploit plant resources are found in all these habitats.

Our species is often described as the ultimate omnivore. But the use of hard-to-acquire but highly rewarding plant foods predicts the narrow diet breadth actually observed among hunters and gatherers. While human

informants can give a list of edible plants as long as the known diets of other primates, relatively few of these foods are taken regularly. Many days following Hadza on foraging trips, and many additional days weighing the food they brought home, have given us a list of nine species regularly used in a year (//ekwa, makalita, panjuko, shumuko, tafabe, undushibe, emberipe, baobab, tamarind). Rather fewer days following !Kung foraging in locations chosen by us (many chosen to see how little food they produce – thus likely to expand recorded diet breadth) nonetheless gave a similarly short list. Hill *et al.* (1987) list ten species taken often enough by Ache to yield foraging data. People primarily exploit a small number of 'staple' foods. In contrast, McGrew *et al.* (1988) observed chimpanzees using 43 species and suspect the use of an additional 41 species, but still describe this as a narrow diet breadth relative to other primates. Tutin and Fernandez (1993) report chimpanzees using 111 plant species (and observed them eating 67% of these, i.e. 74 species). Given the very high returns for human foods shown in Table 6.2, diet breadth theory would lead us to expect a narrower diet than accompanies the low returns obtained by other primates. While the global human catalogue of plant foods may far exceed that of other primates, local human populations are likely to have often been characterised by a narrow diet spectrum.

The authors think it is also now clear that female provisioning of weaned offspring (dependent on the use of rewarding but hard-to-acquire plant foods) challenges hunting as a productive explanation of the path of human evolution and the distinctiveness of our species.

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