12

The Grandmother Hypothesis and Human Evolution

KRISTEN HAWKES, JAMES F. O'CONNELL,
NICHOLAS G. BLURTON JONES, HELEN ALVAREZ,
and ERIC L. CHARNOV

Humans differ from other primates in feeding their offspring long after weaning, and in their extended postmenopausal lifespans. Recent research among contemporary hunter-gatherers suggests that these characteristics are evolutionarily related and tied to the use of low-variance, high-yield resources, such as deeply buried tubers (Hawkes, O'Connell, and Blurton Jones 1989, 1997). Where such foods are available, senior women can provision their daughters' weaned offspring, thereby enhancing the children's survivorship and allowing their daughters to produce more children sooner. The resulting fitness increase for grandmothers favors extended postmenopausal lifespans.

This hypothesis has been tested with comparative data on several life history variables by using recent theoretical and empirical work which links the other life history variables with lifespans across a wide range of animal taxa (Charnov 1991, 1993; Charnov and Berrigan 1991, 1993). If human lifespans are extended because of grandmothering, and life histories are assembled as proposed on the basis of this work, then other features of human life histories (including age at maturity and birth rate) should differ in predictable ways from those of other primates, especially the pongids. Analyses completed so far show that they do (Alvarez, 1999; Hawkes, O'Connell, Blurton Jones, Alvarez, and Charnov 1998; O'Connell et al. 1999).

The grandmother argument challenges a fundamental hypothesis about human evolution, namely that our long childhoods are due to the development of the nuclear family, which evolved when husbands/fathers hunted to support their wives and offspring. Here we summarize the grandmother hypothesis and the life history patterns it may explain, note that it joins other challenges to the hunting hypothesis, and develop alternative predictions about human evolution based on the idea that mother-child food sharing and the grandmothering it permits are among our most important behavioral characteristics.

THE ARGUMENT

Grandmothering and Maternal Tradeoffs

Recognition of the evolutionary importance of grandmothers was stimulated by research among the Hadza, a small population of traditional hunter-gatherers living in the Eastern Rift Valley, northern Tanzania (Blurton Jones et al. 1992; Kohl-Larson 1958; Obst 1912; Woodburn 1968). During several periods of fieldwork beginning in the mid-1980s, detailed quantitative data were collected on Hadza demography, settlement patterns, time allocation, foraging, and food sharing (Blurton Jones et al. 1996, and references therein). Among other things, this work documented the unanticipated industry of senior women (Hawkes et al. 1989), the surprisingly active foraging of children (Blurton Jones et al. 1989), and the effect of children's foraging capabilities on mothers' foraging tactics (Blurton Jones et al. 1994; Hawkes, O'Connell, and Blurton Jones 1995). While women were found to organize their foraging in ways that took advantage of resources children could exploit efficiently, they were also seen to target foods that youngsters could not handle for themselves. They could afford to take these foods only because returns were high enough to cover their children's nutritional needs as well as their own. These same high rates were also earned by postmenopausal women (Hawkes et al. 1989). The help the older women provided by feeding their grandchildren was especially important when child-bearing women cut down their foraging with the arrival of a newborn, indicating a "division of labor" between mothers and grandmothers in the production of surviving youngsters (Hawkes, O'Connell, and Blurton Jones 1997).

Grandmothers and Long Postmenopausal Lifespans

This division of labor suggested a solution to the riddle of menopause in humans. In other apes, maximum lifespan is generally estimated at no more than about 50 years (Harvey and Clutton-Brock 1985). As this threshold is approached, all aspects of physiology, including fertility, decline in tandem. In humans, however, the pattern is quite different: maximum lifespan is nearly 100 years, but fertility in women universally ends in about half that time, well in advance of other aspects of physiological frailty (Pavelka and Fedigan 1991). The question is how natural selection came to favor this distinctly human "postreproductive" component of life history.

Many have assumed that the answer lies in Williams's (1957) suggestion that early termination of fertility would likely evolve when extended maternal care became crucial to offspring survival. Aging mothers who stopped bearing additional offspring and devoted their reproductive effort to insuring the survival of children already born would leave more descendants than those who continued to bear new offspring unlikely to survive mother's death.

This stopping-early hypothesis continues to stimulate useful work (Hill and Hurtado 1991, 1996; Peccei 1995; Rogers 1993; Turke 1997), but there are good

reasons to be skeptical about it. Other primates among whom extended maternal care is vital fail to show the predicted "early" end to fertility. In chimpanzees, for example, available data indicate low survival probabilities for late-borns (Goodall 1986, 1989), yet a substantial fraction of aging females still continue to produce them (Caro et al. 1995). In humans maternal death has large effects on the survival of young offspring (Hill and Hurtado 1991) but life expectancy at last birth is decades longer than those critical years. Among the reasons for questioning the stopping-early hypothesis, the most compelling is that human reproduction does not end early in comparison with other apes. Our reproductive spans are at least as long as those of chimpanzees. The striking difference between us and the other great apes lies in our long average lifespans *after* menopause. Schultz's (1969) often reprinted figure makes the point (Figure 12.1) (see also Hill and Hurtado 1991; Kaplan 1997). This feature, not menopause itself, is the derived human trait.

Long average adult lifespans depend on low average adult mortalities. Adult mortality rates are directly linked to patterns of senescence, those age-related declines in performance readily observed as years advance. Evolutionary explanations for senescence depend on the fact that the force of selection declines with age (Medawar 1952). Because the risks of mortality accumulate over time, there are always fewer individuals in older cohorts for selection to affect. Deleterious mutations expressed before maturity may not be passed on at all; those acting after maturity are removed more slowly. Consequently deleterious effects on adaptive performance accumulate at later ages either because of mutation-selection balance or inter-temporal tradeoffs in reproductive effort (reviewed in Partridge and Barton 1993). Mutation-selection balance is reached when the force of selection is no greater than the mutation rate. Thus deleterious mutations are removed no faster than they arise. Inter-temporal tradeoffs occur because the same genes that have positive effects on fitness at one time in an organism's life history can have negative effects at another. The net result depends on the tradeoff between these opposing effects, and (other things equal) earlier effects weigh heavily. So genes that have positive effects at younger ages may be favored, even though they have negative effects later in life. Those that have positive effects late in life will be disfavored if they have negative early effects. Senescence results from this antagonistic pleiotropy (Williams 1957).

Grandmothering could slow aging by either process. It would strengthen selection against late-acting deleterious mutations by increasing the fitness of longer-lived females through the increased reproductive success of their daughters. It would also change the tradeoffs between opposing effects expressed at different ages. Slower senescence generally comes at the cost of reduced fertility at younger ages (Kirkwood and Rose 1991) as more effort allocated to somatic maintenance leaves less for current reproduction. If ape lifespans are in equilibrium in terms of this tradeoff, then they age early by human standards because mutations that improve adaptive performance at later ages are selected against due to reductions they impose on fertility earlier in life. Regular mother-child food sharing could

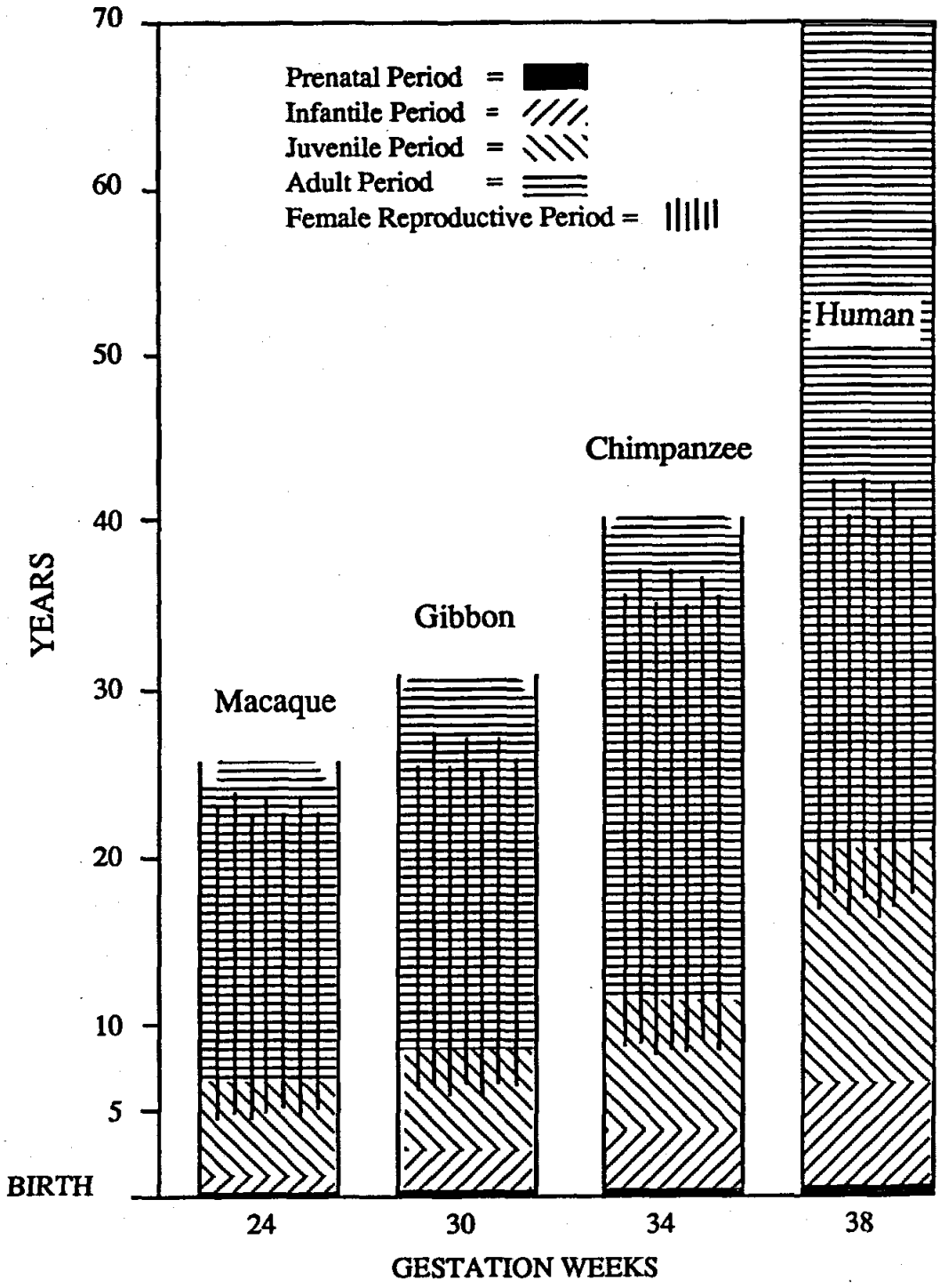

Figure 12.1. Schultz's representation of the length of life history stages in different primate species (redrawn from Schultz 1969).

perturb that equilibrium by increasing the fitness payoffs for late vigor as able senior women earned fitness by feeding grandchildren. Increased somatic effort that slowed aging would allow less allocation to reproduction at younger ages, but the contributions of senior females would increase the reproductive success of childbearers more than enough to offset the reduced expenditure on current reproduction by the childbearers themselves. Continued childbearing, on the other hand, which would conflict with grandmothering, would interfere with this compensation and so be no more favored than in other ape species. According to this model, senescence in all aspects of physiology *except fertility* would be slowed as a result of grandmothering.

Dimensionless Life History Patterns

Recent work in life history theory provides a basis for further development and testing of this argument. Charnov (1991, 1993; Charnov and Berrigan 1991) has shown that life history patterns in large classes of organisms can be characterized by dimensionless invariants, numbers that capture relationships among certain life history variables because they remain constant across large transformations in the variables themselves. To explain these patterns, Charnov assumes stationary populations and so constrains the relationship among three demographic averages: the average rate of offspring production over the adult life span, the average length of adult lifespan, and the probability of offspring survival to maturity. Average adult lifespan sets tradeoffs that determine other life history variables. If grandmothering results in greater longevity, and the tradeoffs in Charnov's mammal model apply, then other aspects of human life history should be affected accordingly.

The mammal model assumes that production can be allocated to growing either oneself or one's offspring. Growth is thus divided into two periods: (1) conception to independence (weaning), where growth is set by mother's production (a function of her size); and (2) independence to maturity (α), where 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.

This model accounts for the correlations long recognized among life history variables and body size (Peters 1983) by tracing them to similarities in the production function. The model also accounts for correlations among life history variables when the effect of body size is removed. Primates, for example, have slow life histories compared with other mammals of similar size (Harvey et al. 1989). Charnov's model draws attention to the low primate A, averaging less than half that of other mammals. Primates thus grow more slowly and have less production

(for a given size) to put into babies. So they are relatively small at a given age of maturity with low fecundity for size (Charnov and Berrigan 1993).

Charnov assumes that, given adult lifespan, selection sets the duration of independent growth (α) according to the tradeoff between (1) the benefits of growing longer, and so having more production to put into offspring; and (2) beginning to reproduce sooner, and so having a greater chance to reproduce before dying. He captures key features of the mortality schedule by assuming an early burst of high mortality that incorporates any density-dependent effects. Mortality then drops to a constant adult level before age of first reproduction. Since the instantaneous adult mortality rate (M) (the inverse of the average adult lifespan) sets the time available to use the gains of growing longer, it determines the optimal age at maturity. As adult lifespan increases (adult mortality rate falls), selection favors delayed maturity to reap the gains of larger size. Thus, both α 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 ($W_0/W_\alpha = \delta$) is approximately constant (Charnov 1993). Since δ scales almost isometrically with body size while production scales up with the growth allometry (a power of about 0.75 [Reiss 1989]), the size of weanlings increases faster with maternal size than does the production 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 model predictions (since confirmed on other, larger data sets [Knobel and van Jaarsveld 1997; Purvis and Harvey 1995]) suggests that it points to real tradeoffs that shape mammalian life histories. Several extensions of the basic model (Charnov 1993; Kozlowski and Weiner 1997) are discussed elsewhere but do not play a role in the comparisons made here. The invariants reveal natural scaling rules: some life history variables are adjusted to others. Fecundity depends on age at maturity; age at maturity is adjusted to adult lifespan. If ancestral human lifespans increased due to grandmothering, then that hypothesis combined with Charnov's mammal model predicts distinctive effects on age at maturity, time or size at weaning, and fertility.

Age at Maturity, Interbirth Intervals, Weaning Weights, and Fecundity

In the dimensionless model, αM is approximately invariant because longer lifespans favor more advanced age at maturity. If fitness gains from growing longer continue to accumulate after menopause, then α should be adjusted to the complete adult life span, not just to the fertile component. Again Schultz's graphic

(Figure 12.1) displays the contrast. Maturity in humans is delayed relative to other apes (Table 12.1). The delay is commensurate with our longer average adult lifespans (1/M). Consequently, αM remains approximately invariant across the hominoids. (Alvarez 1999 considers a larger sample of primate species.)

The grandmother hypothesis further implies that childbearing women will produce babies faster than otherwise expected because of grandmothers' contribution to that production. Human interbirth intervals (IBI) are shorter than those of other great apes (Table 12.1)—one thing *wrong* in Schultz's classic comparison (Figure 12.1). In principle, grandmothers might contribute to this pattern in either, or both,

Table 12.1. Average Values for Selected Life History Variables

	Average Adult Lifespan[1] *(1/M)*	*Age at Maturity*[2]	*Age at Weaning*[3]	α[4]	αM	*Ratio of Weight at Weaning/ Adult Weight*[5] δ	*Daughters/ Year*[6] *b*	αb
Orangutans	17.9	14.3	6.0	8.3	.46	.28	.063	0.52
Gorillas	13.9	9.3	3.0	6.3	.45	.21	.126	0.79
Chimpanzees	17.9	13.0	4.8	8.2	.46	.27	.087	0.70
Humans	32.9	17.0	2.8	14.5	.44	.21	.142	2.05

Notes

1. The method described in Charnov 1993:194 (caption to figure 5.6) is used to estimate average adult lifespan (1/M) from maximum observed lifespans (T_{max}): $1/M = 0.4T_{max} - 0.1$. Values for orangutans: Leighton et al. 1995; gorillas: Stewart et al. 1988; chimpanzees: Nishida et al. 1990. The human value is estimated from Howell's (1979) oldest observed !Kung individual (aged 88) and Hill and Hurtado's (1996) oldest observed (forest-living) Ache individual (aged 77).
2. Age at first birth minus gestation. Orangutans: Leighton et al. 1995; gorillas: Stewart et al. 1988; chimpanzees: the mean of the means from Wallis (1997) for Gombe, Nishida et al. 1990 for Mahale, and Sugiyama 1994 for Bossou; humans: the mean of the mode for !Kung in Howell 1979 and Ache in Hill and Hurtado 1996.
3. 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.
4. Defined as the period of independent growth, from weaning to maturity.
5. Data from Lee et al. (1990) 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 55kg (the upper end of the range for modern foragers who are generally smaller that either contemporary nonforagers or pre-Mesolithic moderns). We use 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) to represent humans.
6. Great ape data from Galdikas and Wood (1990), who reappraise birth spacing in all species in the same way. We use medians calculated therein (for closed intervals) plus two months to approximate the mean interval; then divide by 2 to get the rate in daughters. Galdikas and Wood use the Gainj, a population of horticulturalists in highland Papua New Guinea, to represent humans, for which $b = 0.132$. We use the mean of the !Kung (Howell 1979) and the Ache (Hill and Hurtado 1996).

of two ways: (1) by feeding lactating mothers and their still-nursing infants, thereby adding to the production that goes into babies, who then grow to independence faster; (2) by substituting shared food for mother's milk, thereby allowing mothers to wean their infants before they reach independence.

The second option is suggested by the Hadza patterns: grandmothers provision weaned grandchildren directly (Hawkes, O'Connell, and Blurton Jones 1997). If this practice were common in an ancestral human population, then it could have allowed mothers to wean infants early and at lower body weights (Hawkes, O'Connell, Blurton Jones, Alvarez, and Charnov 1998). Weaning would then mark a shift to grandmother's support, not feeding independence. If so, then δ (the ratio of weaning weight to adult weight) should be low for humans relative to its values among other apes.

As expected on the basis of the grandmother hypothesis, human δ is lower than that for chimpanzees and orangutans. However, it is not lower than that for gorillas. Here we note two of the possible reasons for this failure of our expectation. First, the relatively low δ for gorillas could be a reflection of the body size trend across the primates. Although the dimensionless model takes δ to be approximately constant, the ratio actually varies slightly, and negatively, with maternal size in both primates and other mammals (Charnov 1993; Purvis and Harvey 1995; cf. Knobel and van Jaarsveld 1997). The average δ for the primate order is around 0.33 (Charnov 1993:fig. 5.4). All great apes have δ values lower than the primate mean (Table 12.1). The sample of apes is too small and too skewed by body size itself to allow a meaningful test of systematic effects of maternal size on δ; but, given the trend of decreasing δ with body size across the order, we might expect a grandmotherless ape of human size to wean at a greater relative size than do the much larger gorillas.

A second possibility is that the human δ value reported in Table 12.1 (0.21), derived from a sample of two modern foraging populations, may be too high. Lee et al. (1990) report much greater variation in adult than weanling weights in humans. Ethnographically known foragers are small by pre-Mesolithic human standards. The human maternal and weaning weights provided by Lee and colleagues come from a sample not restricted to foragers. The larger adult size might be more representative of Paleolithic moderns. It gives a δ of 0.16, well below that for any of the great apes.

Other comparisons of primate weaning patterns are pertinent here. More than a decade ago, Lefebvre (1985) developed, tested, and rejected an early-weaning hypothesis. He suggested that food sharing might be an alternative that allowed mothers to save the metabolic costs of lactation as well as the cost of delayed fertility imposed by lactational amenorrhea. In his sample, however, weaning age was no earlier for the two species of primates (chimpanzees and golden-lion tamarins) where parent-offspring food sharing is reported to be more frequent than for other nonhuman primates. He also noted that human weaning age did not differ from the general primate pattern when regressed on adult weight, gestation length, and age at maturity.

Lefebvre's focus was on weaning age, while δ pertains to size. In Charnov's mammal model, size varies with time, but rate of growth to weaning depends on the production function and so on both the coefficient A and the allometric exponent c. Since A is even lower for humans than for other primates (Hill and Hurtado 1996), we require more time to reach a given size, or to grow offspring to a given size, than do other species in the order. A human mother nursing her baby for the same amount of time (Lefebvre's measure) as the average nonhuman primate of similar size "grows" it less. The addition of grandmother's production could accelerate infant growth (faster than expected, given our A), or acceleration could be combined with some reduction in weaning size as grandmother takes over production (see analysis across a larger sample in Alvarez 1999).

The relatively high fertility of humans is actually much greater than suggested by direct comparison of IBIs with other hominoids. Across all mammals, including primates, fecundity (b) scales negatively with age at maturity. αb is approximately invariant. But if later maturity in humans is due to grandmothering, then grandmother's contribution to production should have important countervailing effects that increase b. The αb value for humans is more than double those of the other large-bodied apes (Table 12.1). As the grandmother hypothesis predicts, 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.

Combined with Charnov's mammal model, the grandmother hypothesis predicts several distinctive features of human life history, including long lifespans after menopause, late age at maturity, short interbirth intervals, and high fertility. Other hypotheses have been offered to account for each of these individually (Hill 1993; Smith and Tompkins 1995), but grandmothering may explain all of them simultaneously.

IMPLICATIONS

The grandmother hypothesis suggests a different model of human evolution than the conventional one that makes men's big game hunting and provisioning of mates and offspring the keystone human adaptation. Wide reliance on the hunting model continues in spite of accumulating reasons to reject it. Here we summarize its principle features and review critical shortcomings; then we outline an alternative argument about evolutionary transitions based on the grandmother hypothesis and identify some possible archaeological tests.

The Hunting Hypothesis: Review and Critique

According to the hunting hypothesis, ancestral males took up hunting to provide for their mates and children (Washburn and Lancaster 1968). Provisioning fathers made nuclear families basic social units; the sexual division of labor

permitted greater investment in children over longer periods of time (Lancaster and Lancaster 1983). This increased investment was favored because it allowed the development of improved cognitive and social skills and more social learning. Enhanced capacities for cooperation increased the advantages for males allied with kin to ensure the support and protection of their families. Uniquely human patterns of group composition and social behavior emerged as a result.

The appeal of this model lies in its capacity to incorporate widely held ideas about human sociality and cognition, account for contrasts between human behavior and that of other primates, and draw support from the archaeological and hominid fossil records. Nonhuman primate males do not provision offspring; persistent, exclusive consort relationships are all but absent in communities with multiple males. By contrast, among all ethnographically known human foragers, men hunt, women gather, and nuclear families are evident social and reproductive units. The support of hunting fathers is presumed to fund longer juvenile dependence, which allows the elaborated learning and cognitive complexity that results in the broad geographical dispersal, expanded tool kits, and distinctive social traditions typical of humans. The putative material signature of this pattern, the association of stone tools with the bones of large animals at central places, dates to the beginning of the archaeological record, and coincides broadly with the origin of genus *Homo* itself (Klein 1999). For many, this makes men's hunting and meat sharing the fundamental framework around which all other aspects of human evolution were subsequently organized (Isaac 1978).

This picture is so compelling that disputes within paleoanthropology over the past few decades have centered not on its basic features, but on when the characteristics it embodies first emerged. Initial arguments linked male provisioning with bipedalism, hunting, and the use of stone tools, and dated all of them to the beginning of the Pleistocene (Isaac 1978). This formulation was undercut by the demonstration that bipedality preceded clear evidence of either hunting or stone tool use by millions of years (Johanson and White 1979). Subsequent arguments placed the onset of male provisioning at one or another of several different points in the record, including the early Pliocene (Lovejoy 1981), based primarily on the date for bipedality; the Plio-Pleistocene boundary (Bunn and Kroll 1986), based on possible evidence for the transport of large animal body parts to central places; and the mid-Upper Pleistocene (Binford 1985; Soffer 1992), based on a different interpretation of the animal body part data and other archaeological evidence read to indicate the presence of nuclear family households. Where the date assigned is late, patterns in human or hominid social organization and food acquisition that prevailed earlier, and were sufficiently distinct from those of other primates to account for the formation of the archaeological record, remain essentially unimagined (O'Connell 1995).

The resilience of the hunting model is especially impressive in light of the weaknesses recently revealed in the proposed link between hunting and paternal provisioning. Chimpanzees have been shown to hunt much more frequently and

successfully than previously supposed (Boesch and Boesch 1989; Stanford 1996, 1999; Wrangham and Bergman-Riss 1990). As with humans, hunting is a male specialty and the meat obtained is widely shared; yet chimps lack nuclear families, paternal provisioning, a sexual division of labor, and extended childhoods. The proposition that these are the evolutionary products of male hunting and meat sharing is accordingly undercut.

The assumption that human males hunt to provision their families has also been challenged. Recent work among tropical hunter-gatherers shows that "encounter" hunting (sensu Binford 1980) is a risky business, even with relatively sophisticated projectile weapons. Among the Hadza, for example, where average rates of meat consumption are high, individual hunters fail to kill or scavenge large game on 97% of all hunting days (Hawkes et al. 1991). When a hunter is successful, the meat is widely shared, most going to individuals outside his nuclear family rather than to his own wife and children. Other strategies that would provision families more reliably with meat (small game hunting and trapping) are consistently ignored. Hunters would supply even more calories to their households by plant food collecting (Hawkes 1993). Similar patterns are observed among other low-latitude hunting populations where hunting supplies a collective good from which all benefit, regardless of their relationship with the hunter (Hawkes 1990). It is women's foraging, not men's hunting, that differentially affects an individual family's nutritional welfare.

Questions can also be raised about another key element of the hunting hypothesis: the notion that longer childhoods are favored because they expand human technological and social capacities and skills. While it is now widely appreciated that humans are not the only tool-using animals, our dependence on technology has long been assumed to result from feedback between hunting and the extended childhoods for learning locally efficient tactics of resource acquisition that hunting fathers support. But recent studies of modern hunter-gatherers indicate wide variation in the ages at which children begin to forage, even in broadly similar ecological circumstances (Blurton Jones et al. 1989, 1994). There is no indication that it takes long years of practice to acquire human foraging skills (Blurton Jones et al. 1997).

The hunting hypothesis also includes the proposition that social learning was uniquely favored in humans when local groups of hunters cooperated to support and protect their mates and dependent offspring (e.g., Alexander 1990). Arguments about the selection pressures that social life places on the evolution of intelligence (e.g., Humphrey 1976) have drawn attention to the sophisticated capacities for social manipulation that characterize primates generally (Byrne and Whiten 1988). Both competition for resources and the advantages of alliances (Harcourt and de Waal 1992) usually increase with group living, so the differences in social intelligence between humans and other hominoids, to say nothing of differences among species of nonhuman primates or social mammals generally, require additional explanation.

A comparative picture that includes nonprimate and nonmammalian taxa does not support the supposition that long juvenile periods require increased parental investment, or that delayed maturity generally results in greater brain size when the effects of body size are controlled (Austad and Fischer, 1992; Charnov 1993; Harvey et al. 1979). Species with small brains may also have late ages of maturity for their size. Our long juvenile periods *may* have evolved for uniquely human reasons. But that can only be established if more general explanations fail.

Finally, the inference that coalitions of male kin form the usual core of human and more generally hominid foraging communities is also open to question. Paired with the fact that male philopatry is the common pattern among chimpanzees, the patrilocality of hunter-gatherers stimulated the hypothesis that female natal dispersal has characterized all descendants of our common ancestor (Foley and Lee 1989; Rodseth et al. 1991; Wrangham 1987). The idea that modern human hunters are typically patrilocal dates at least to the early part of this century (Kelly 1995). It was briefly overturned in the wake of *Man the Hunter* (Lee and DeVore 1968), because the best studied cases discussed there were not patrilocal. Subsequently, the older view was resurrected by Ember's (1978) tabulation of a larger sample of cases showing patrilocality to be the most common residential arrangement. The variation shown in these data is substantial: patrilocality is actually less frequent among non-equestrian, non-fishing-dependent hunters than in the societies in Murdock's (1967) *Ethnographic Atlas* sample as a whole (56% vs. 71%).

Although humans might be expected to display more variation in social organization with local ecology than any nonhuman primate species, the other descendants of our common ancestor with *Pan* vary much more than the widely repeated generalizations suggest. Among bonobos, where females form larger, more cohesive groups than do common chimpanzees, males do not display the territorial kin-based coalitions seen in the latter (Wrangham and Petersen 1996). Patterns of natal dispersal among chimpanzees vary within and between study sites. Five of the eleven resident female adults in the habituated population at Gombe did not emigrate at maturity (Pusey et al. 1997). Fifi, an especially famous illustration, staying with her mother Flo, has logged the highest reproductive success ever recorded for a free-living chimpanzee (Goodall 1986; Pusey et al. 1997). At Tai, dispersal patterns are not yet documented, but the recent report that more than half the infants were not sired by resident males (Gagneux et al. 1997) raises fundamental questions about male territorial alliances and suggests the possibility of low rates of female dispersal there as well. In the small chimpanzee population at Bossou, Guinea, male migration (often assumed to be ruled out in this species because stranger males would be killed by residents elsewhere) has been more frequent than female (Sugiyama and Koman 1979). A visit by stranger males at this site generated great excitement, but no aggression from the resident males. In captivity, male chimpanzees show remarkable interest and facility in constructing and manipulating alliances with unrelated stranger males (de Waal 1982), patterns consistent with an evolutionary history in which those capacities were often useful.

The Grandmother Hypothesis: A Comprehensive Alternative

These various challenges notwithstanding, the hunting hypothesis continues to form the core of most arguments about human evolution, largely, in our view, because of the absence of an alternative. The grandmother hypothesis provides one. Three directions can be nominated for future work.

Local Group Composition. The grandmother hypothesis focuses attention on mother-child food sharing and the fitness payoffs available to coresident mothers and daughters that arise when resources that young juveniles cannot handle efficiently become important in the diet. As daughters grow, they acquire the strength and skill needed to help feed their younger siblings. When they mature, the assistance of aging mothers continues to enhance the benefits of proximity. From this perspective, long postmenopausal lifespans, late age at maturity, and high fertility suggest an ancestral pattern of co-residence among related females.

The ethnographic record shows that among foragers the tendency toward matrilocality increases with women's relative contribution to subsistence and (separately) with increased dependence on gathering (Ember 1975). The grandmother hypothesis should stimulate increased attention to the activities of older women and explicit examination of the spatial proximity of mothers and daughters. Even in cases classified unequivocally as patrilocal, female kin may often be co-residents and senior women contribute to the domestic workload of their daughters (e.g., Denham 1974; O'Connell, unpublished Alyawara data).

Grandmothers can certainly enhance their fitness by aiding sons, but evidence of grandmothering effects on human life histories points more strongly to mothers helping daughters. Mothers and daughters face similar tradeoffs, whereas sons must invest in mating competition (Hawkes, Rogers, and Charnov 1995). A food-sharing mother might attract females to her son's group, but this would not assure her son paternity of those females' offspring. His fitness would depend on his success in competing with other males. Winners of that competition would enjoy higher reproductive success whether or not their mothers contributed to the fertility of their mates. Even if a grandmother could identify her son's offspring and single out grandchildren to feed, her potential fitness gains through increased fertility of "daughters-in-law" would be devalued by the uncertain paternity of subsequent children more quickly born to the mothers of those grandchildren.

Molecular studies may provide evidence about ancestral social organizations. Sex-biased patterns of dispersal can have characteristic effects on the relative variation of mitochondrial and nuclear genes in descendant populations. The grandmother hypothesis provides a rationale for the modeling needed to identify critical tests. According to one suggestive appraisal, patterns of variation in "small aboriginal populations indicate that their genetic structure and levels of female dispersal are similar to those in macaque populations," where males but not females

usually disperse (Melnick and Hoelzer 1993:8). Further development of this approach is clearly in order.

Extended Juvenile Periods and Social Learning. Primates generally have long juvenile periods compared with mammals of the same adult body size (Harvey et al. 1989). If maturity is delayed when adult mortalities are low as explained in Charnov's mammal model, then primate social intelligence could result as the "waiting time" is allocated to serve the juvenile's fitness. Drawing the causal arrow from late maturity to learning (Janson and van Schaik 1993), instead of the other way around, may help explain the differences in cognitive elaboration between primates and other mammals (who, on average, have shorter juvenile periods for their body sizes, and face less within group competition), and also the differences among primate species, especially between humans and other apes.

Evolutionary Scenarios. In principle, we expect grandmothering to have been favored under ecological conditions that promoted use of resources that yield high return rates to adults but that youngsters cannot handle efficiently on their own. Taking a lead from the Hadza case, such resources might have included (though need not have been limited to) tubers that require substantial upper body strength and endurance to collect, and various forms of treatment (especially roasting) to eliminate toxins and improve palatability and nutrient yield (see also Coursey 1973; Stahl 1984). Though tubers with these qualities are commonly exploited by ethnographically known hunter-gatherers worldwide, they are generally unimportant, if not entirely absent, in the diets of most other primates (Whiten and Widdowson 1992). They may have entered human or hominid diets initially either as a function of technological innovations that improved handling efficiency (e.g., adoption of digging sticks, development of controlled use of fire) or as a result of declines in the availability of less expensive resources previously favored. Such declines may have been caused by changes in climate, especially increased aridity and seasonality, and would in themselves have favored technological changes that improved efficiency in the exploitation of resources previously ignored (Hawkes and O'Connell 1992).

As these new resources were adopted and the offspring provisioning they allowed became established, contingent adjustments in life history and ecology should have followed accordingly. Relatively small size at weaning, delayed maturity, and reduced rates of senescence in all aspects of physiology except fertility should have been among the results. Shorter IBI and relaxed density-dependent effects on juvenile mortality (Charnov 1991, 1993; Hill and Hurtado 1996) may have stimulated sharp increases in local population densities. Use of tubers in particular may have permitted use of highly seasonal (especially arid) habitats previously unexploited because of the inability of juveniles to feed themselves there efficiently.

Currently available data strongly suggest that australopithecines and the earliest representatives of genus *Homo* had life histories comparable to those of modern

pongids (Smith and Tompkins 1995). Subsequent adjustments in the direction of the modern human pattern, coincident with at least some of the proposed ecological and technological correlates, are evident at least three points in the prehistoric record:

1. The initial appearance of *Homo erectus* (more narrowly, *ergaster*) about 1.8 million years ago (Feibel et al. 1989) is associated with the acceleration of a long-term global climatic trend toward cooler, drier, more seasonal conditions and the expansion of savanna habitats (deMenocal 1995). *H. erectus* displays evidence for delayed maturity relative to earlier hominids (Walker and Leakey 1993; Clegg and Aiello 1999), significant expansion of geographical range (Swisher et al. 1994), and (highly controversial) evidence for the use of fire (Gowlett et al. 1981). The possibility that grandmothering explains the evolution of *Homo erectus* is explored in detail in O'Connell et al (1999).
2. Early archaic *Homo sapiens* (up to 600,000 years ago; Clark et al. 1994) appears in the wake of a further shift toward cool, dry climates and is more widely distributed than previous forms, notably in cool temperate habitats in various parts of Eurasia (Roebrucks et al. 1992). Controlled use of fire is more clearly indicated, at least among later populations (James 1989). Maturity may be delayed longer than in *erectus* (Tompkins 1996), although recent work suggests that age at maturity in *erectus* may have been in the modern range (Clegg and Aiello 1999).
3. The dispersal of anatomically modern *Homo sapiens* (about 50,000 years ago) begins shortly after the sudden onset of the last glaciation. Not long ago some paleoanthropologists hypothesized that fully modern life histories appeared only with our species (Trinkhaus and Tompkins 1990), which enjoys unprecedented success in the exploitation of arid habitats, especially at high latitudes (Klein 1995).

Further research is clearly required to determine the point at which modern human life histories and the adaptive advantages they provide first became established. The complexity of the record suggests diversity among hominids that has no modern counterpart. There is no reason to suppose that life history patterns must take either the modern human form or that of modern great apes. If the grandmotherless great ape pattern is one equilibrium, and the modern human pattern is another, what might set—and what perturb—additional equilibrium points? Answers to this question may offer leverage for explaining the diversity among hominids. [Recent reappraisal of the record (Wood and Collard 1999a,b) holds out hope of simplifying some of the diversity.]

Male Strategies. In focusing attention on links among female foraging strategies and features of female life history, the grandmother hypothesis may seem to be silent on males. But changes in the foraging strategies of women should have significant effects on the tradeoffs faced by men. For example, differences in the size of female groups, a variable directly related to feeding competition, have important consequences for male strategies in other apes (Wrangham et al. 1996).

Feeding competition among females should decline if extractive requirements, rather than resource density, limit return rates. If mothers and daughters also benefit from sharing food, larger and more cohesive groups should be common. The changes in female group size, foraging range, and the habitat expansion predicted to occur in association with grandmothering should therefore alter the competitive arena for males.

One effect that the grandmother hypothesis could have on the investigation of male strategies is indirect. Since male provisioning is not required to account for our late maturity and high fecundity, this gives additional weight to the ethnographic observations that hunters are not supporting their families (Hawkes 1990, 1993; Hawkes et al. 1991). Wider appreciation that paternal provisioning is not ubiquitous among foragers should invite alternative explanations for the long-term pairing of husbands and wives characteristic of humans. Mating patterns vary among the great apes, but all display clear male hierarchies in which high-ranking males succeed in claiming disproportionate mating access to fertile females (Furuichi and Ihobe 1994; van Schaik and van Hoof 1996; Watts 1996). In contrast, human foraging societies are often "egalitarian" (Boehm 1993; Fried 1967), and most adult men successfully claim mating priority for a particular wife. Because of assumptions about the central role of paternal provisioning, mating competition has been deemed less important among human males (cf. Chagnon 1979). More attention paid to it should generate novel hypotheses about both the origins and maintenance of marriage (Hawkes 2000; Blurton Jones et al., Chapter 4, this volume).

Given that most adults do marry, the life history patterns associated with grandmothering have an additional implication. With long postmenopausal lifespans, the age profile of fertility no longer coincides with aging in most aspects of female adaptive performance. General health and competence become poor fecundity cues. Male preference for young partners, which sharply distinguishes men (Jones 1996) from chimpanzees (Morin 1993), could be favored as a consequence.

Combined with a dimensionless approach to life histories, the grandmother hypothesis shows that several distinctive human characteristics may be systematic variations on a general primate pattern. Novel ancillary predictions about behavioral patterns in the modern world, as well as in the past, follow. The development of theoretically warranted hypotheses quite different from those currently favored should contribute to our understanding of human evolution, whatever the outcome of further tests.

SUMMARY

1. Humans are unique among the great apes for the importance of mother-child food sharing and long postmenopausal lifespans. We elaborate a grandmother hypothesis that identifies an evolutionary link between these features. Combined with a model of mammalian life histories, the hypothesis explains our

long lifespans with mid-life menopause, and also the late age at maturity, and high fertility that distinguish humans from the other apes.

2. Without food sharing, mothers accompanied by young juveniles are tied to resources that youngsters can handle effectively for themselves. Sharing releases mothers to exploit resources that give high return rates to adults but not young children. The same high return resources allow other adults to help mothers feed dependent toddlers. Grandmothers who provide such help increase their own genetic success because their daughters can have more babies sooner. This division of labor between older women and their younger kin would strengthen selection against senescence in all aspects of physiology except fertility.

3. Some predictions of the grandmother hypothesis are tested by comparing human life history averages to those of the other great apes using Charnov's model of life history invariants. Life history traits vary widely with body size, but they remain correlated with each other even when body size is removed. Charnov's model explains the invariant relationship between key pairs of life history traits across transformations of body size and phylogeny. In his model adult mortalities (M) (the inverse of average adult lifespans) determine the optimal age at maturity (α) and rate of births (b). If long human lifespans are a consequence of grandmothering, and Charnov's model is approximately correct, then our age of maturity should be adjusted to the entire lifespan, not just the period from maturity to menopause; and our fertility rates should reflect the contribution of both mothers and grandmothers. Comparisons with the other hominoids show that human αM and αb values are consistent with this reasoning. The results show that grandmothering can explain a cascade of adjustments long attributed to other causes.

4. The grandmother hypothesis challenges the popular model in which men's hunting to provision wives and offspring is key to the evolution of distinctively human patterns of social organization and child development. Although the hunting hypothesis has been criticized from many directions, scenarios of human evolution continue to use it routinely in the absence of a comprehensive alternative. The grandmother hypothesis, with the life history adjustments it can explain, is such an alternative. We briefly consider implications for a range of ideas about the human past.

ACKNOWLEDGMENT

We thank Ursula Hanly for redrafting the figure from Schultz 1969.

REFERENCES

Alexander, R. D. 1990. *How Did Humans Evolve? Reflections on the Uniquely Unique Species.* University of Michigan Museum of Zoology, Special Publication No. 1. Ann Arbor.

Alvarez, H. 1999. The grandmother hypothesis and primate life histories. Ms., Department of Anthropology, University of Utah, Salt Lake City (submitted for publication).

Austad, S. N., and K. E. Fischer. 1992. Primate longevity: Its place in the mammalian scheme. *American Journal of Primatology* 28:251–261.

Binford, L. 1980. Willow smoke and dogs' tails: Hunter-gatherer settlement systems and archaeological formation processes. *American Antiquity* 45:4–20.

———. 1985. Human ancestors: Changing views of their behavior. *Journal of Anthropological Archaeology* 4:292–327.

Blurton Jones, N. G., K. Hawkes, and P. Draper. 1994. Foraging returns of !Kung adults and children: Why didn't !Kung children forage? *Journal of Anthropological Research* 50:217–248.

Blurton Jones, N. G., K. Hawkes, and J. F. O'Connell. 1989. Studying costs of children in two foraging societies: Implications for schedules of reproduction. In *Comparative Socioecology of Mammals and Man,* V. Standon and R. Foley, eds. Pp. 365–390. London: Blackwell.

———. 1996. The global process and local ecology: How should we explain differences between the Hadza and the !Kung? In *Cultural Diversity among Twentieth Century Foragers: An African Perspective,* S. Kent, ed. Pp. 159–187. Cambridge: Cambridge University Press.

———. 1997. Why do Hadza children forage? In *Uniting Psychology and Biology: Integrative Perspectives on Human Development,* N. Segal, G. E. Weisfeld, and C. C. Weisfeld, eds. Pp. 279–313. Washington, D.C.: American Psychological Association.

Blurton Jones, N. G., L. C. Smith, J. F. O'Connell, K. Hawkes, and C. Kamazura. 1992. Demography of the Hadza, an increasing and high density population of savanna foragers. *American Journal of Physical Anthropology* 89:159–181.

Boehm, C. 1993. Egalitarian society and reverse dominance hierarchy. *Current Anthropology* 34:227–254.

Boesch, C., and H. Boesch. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology* 78:547–573.

Bunn, H. T., and E. Kroll. 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge. *Current Anthropology* 27:257–272.

Byrne, R. and A. Whiten, eds. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans.* Oxford: Clarendon Press.

Caro, T. M., D. W. Sellen, A. Parish, R. Frank, D. M. Brown, E. Voland, and M. Borgerhoff Mulder. 1995. Termination of reproduction in nonhuman and human female primates. *International Journal of Primatology* 16:205–220.

Chagnon, N. 1979. Is reproductive success equal in egalitarian societies? In *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective,* N. Chagnon and W. Irons, eds. Pp. 374–401. North Scituate, Massachusetts: Duxbury Press.

Charnov, E. L. 1991. Evolution of life history variation in female mammals. *Proceedings of the National Academy of Sciences* (USA) 88:1134–1137.

———. 1993. *Life History Invariants: Some Explanations of Symmetry in Evolutionary Ecology.* Oxford: Oxford University Press. Charnov, E. L., and D. Berrigan. 1991. Dimensionless numbers and the assembly rules for life histories. *Philosophical Transactions of the Royal Society* (London), Series B 33:241–248.

———. 1993. Why do female primates have such long lifespans and so few babies? or Life in the slow lane. *Evolutionary Anthropology* 1:191–194.

Clark, J. D., B. Asfaw, G. Assefa, J. W. K. Harris, H. Kurashina, R. C. Walter, T. D. White, and M. A. J. Williams. 1994. Paleoanthropological discoveries in the Middle Awash Valley, Ethiopia. *Nature* 307:423–428.

Clegg, M. and L. Aiello. 1999. A comparison of the Nanokotoma *Homo Erectus* with juveniles from a modern human population. *American Journal of Physical Anthropology* 110(1):81–93.

Coursey, D. G. 1973. Hominid evolution and hypogeous plant foods. *Man* 8:634–635.
deMenocal, P. B. 1995. Plio-Pleistocene African climate. *Science* 270:53–59.
de Waal, F. 1982. *Chimpanzee Politics: Power and Sex among the Apes.* New York: Harper and Row.
Denham, W. W. 1974. Infant transport among the Alyawara tribe, central Australia. *Oceania* 44:253–277.
Ember, C. 1975. Residential variation among hunter-gatherers. *Behavioral Science Research* 3:199–227.
———. 1978. Myths about hunter-gatherers. *Ethnology* 4:439–448.
Feibel, C. S., F. H. Brown, and I. MacDougal. 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* 78:595–622.
Foley, R., and P. Lee. 1989. Finite social space, evolutionary pathways, and reconstructing hominid behavior. *Science* 243:901–906.
Fried, M. H. 1967. *The Evolution of Political Society.* New York: Random House.
Furuichi, T., and H. Ihobe. 1994. Variation in male relationships in bonobos and chimpanzees. *Behaviour* 130:211–228.
Gaganeux, P., D. S. Woodruff, and C. Boesch. 1997. Furtive mating in female chimpanzees. *Nature* 387:358–359.
Galdikis, B., and J. Wood. 1990. Birth spacing patterns in humans and apes. *American Journal of Physical Anthropology* 63:185–191.
Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge: Harvard University Press.
———. 1989. Gombe: Highlights and current research. In *Understanding Chimpanzees,* P. Heltne and L. Marquardt, eds. Pp. 2–21. Cambridge: Harvard University Press.
Gowlett, J. A. J., J. W. K. Harris, D. Walton, and B. A. Wood. 1981. Early archaeological sites, hominid remains, and traces of fire at Chesowanja, Kenya. *Nature* 294:125–129.
Harcourt, A. H., and F. B. M. de Waal, eds. 1992. *Coalitions and Alliances in Humans and Other Animals.* Oxford: Oxford Scientific.
Harvey, P. H., and T. Clutton-Brock. 1985. Life history variation in primates. *Evolution* 39:559–581.
Harvey, P. H., D. E. L. Promislow, and A. F. Read. 1989. Causes and correlates of life history differences among mammals. In *Comparative Socioecology of Mammals and Man,* V. Standen and R. Foley, eds. Pp. 305–318. London: Blackwell.
Hawkes, K. 1990.Why do men hunt? Some benefits for risky strategies. In *Risk and Uncertainty,* E. Cashdan, ed. Pp. 145–166. Boulder: Westview Press.
———. 1991. Showing off: Tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology* 12:29–54.
———. 1993. Why hunter-gatherers work: An ancient version of the problem of public goods. *Current Anthropology* 34:341–361.
———. 2000. Big game hunting and the evolution of egalitarian societies. In *Hierarchies in Action: Cui Bono?* M. Deihl, ed. Center for Archaeological Investigations, Occasional Paper No. 27, pp. 59–83. Southern Illinois University.
Hawkes, K., and J. F. O'Connell. 1992. On optimal foraging models and subsistence transitions. *Current Anthropology* 33:63–66.
Hawkes, K., J. F. O'Connell, and N. G. Blurton Jones. 1989. Hardworking Hadza grandmothers. In *Comparative Socioecology of Mammals and Man,* V. Standen and R. Foley, eds. Pp. 341–366. London: Blackwell.
———. 1991. Hunting income patterns among the Hadza: Big game, common goods, foraging goals, and the evolution of the human diet. *Philosophical Transactions of the Royal Society,* Series B 334:243–251.
———. 1995. Hadza children's foraging: Juvenile dependency, social arrangements and mobility among hunter-gatherers. *Current Anthropology* 36:688–700.

———. 1997. Hadza women's time allocation, offspring production, and the evolution of long postmenopausal life spans. *Current Anthropology* 38:551–577.

Hawkes, K., A. R. Rogers, and E. L. Charnov. 1995. The male's dilemma: Increased offspring production is more paternity to steal. *Evolutionary Ecology* 9:1–16.

Hawkes, K., J. F. O'Connell, N. G. Blurton Jones, H. Alvarez, and E. L. Charnov. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences* 95 (3):1336–1339.

Hill, K. 1993. Life history theory and evolutionary anthropology. *Evolutionary Anthropology* 2:78–88.

Hill, K., and A. M. Hurtado. 1991.The evolution of reproductive senescence and menopause in human females: An evaluation of the grandmother hypothesis. *Human Nature* 2:313–350.

———. 1996. *Ache Life History: The Ecology and Demography of a Foraging People.* New York: Aldine de Gruyter. Howell, N. 1979. *Demography of the Dobe !Kung.* New York: Academic Press.

Huang W., R. Ciochon, Y. Gu, R. Larick, Q. Fang, H. Schwarcz, C. Yonge, J. De Vos, and W. Rink. 1995. Early *Homo* and associated artifacts from Asia. *Nature* 378:275–278.

Humphrey, N. K. 1976. The social function of intellect. In *Growing Points in Ethology,* P. G. Bateson and R. A. Hinde, eds. Pp. 303–317. Cambridge: Cambridge University Press.

Isaac, G. Ll. 1978. The food sharing behavior of protohuman hominids. *Scientific American* 238(4):90–108.

James, S. 1989. Hominid use of fire in the Lower and Middle Pleistocene: A review of the evidence. *Current Anthropology* 30:1–26.

Janson, C. H., and C. P. van Schaik. 1993. Ecological risk aversion in juvenile primates. In *Juvenile Primates: Life History, Development and Behavior,* M. E. Periera and L. A. Fairbanks, eds. Pp. 57–76. Oxford: Oxford University Press.

Johanson, D., and T. D. White. 1979. A systematic asessement of early African hominids. *Science* 203:321–330.

Jones, D. 1996. An evolutionary perspective on physical attractiveness. *Evolutionary Anthropology* 5:97–109.

Kaplan, H. 1997. The evolution of the human life course. In *Between Zeus and the Salmon,* K. W. Wachter and C. E. Finch, eds. Pp. 175-211. Washington, DC: National Academy Press.

Kelly, R. L. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways.* Washington, D.C.: Smithsonian Institution.

Kirkwood, T. L. L., and M. R. Rose. 1991. Evolution of senescence: Late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society,* Series B 332:15–34.

Klein, R. G. 1995. Anatomy, behavior, and modern human origins. *Journal of World Prehistory* 9:167–198.

———. 1999. *The Human Career: Human Biological and Cultural Origins* (2nd ed.) Chicago: University of Chicago Press.

Knobel, D. L., and A. S. van Jaarsveld. 1997. Mammalian life-history evolution: An evaluation of Charnov's model. Ms., Department of Zoology and Entomology, University of Pretoria.

Kohl-Larson, L. 1958. *Wildbeuter in Ost-Afrika: Die Tindiga, ein Jager-und Sammlervolk.* Berlin: Dietrich Reimer.

Kozlowski, J., and J. Weiner. 1997. Interspecific allometries are by-products of body size optimization. *American Naturalist* 149:352–380.

Lancaster, J., and C. Lancaster. 1983. Parental investment: the hominid adaptation. In *How Humans Adapt,* D. Ortner, ed. Pp. 33–69. Washington, D.C.: Smithsonian Institution Press.

Lee, R. B., and I. DeVore, eds. 1968. *Man the Hunter.* Chicago: Aldine.

Lee, P. C., P. Majluf, and I. J. Gordon. 1990. Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology* 225:99–114.

Lefebvre, L. 1985. Parent-offspring food sharing: A statistical test of the early weaning hypotheis. *Journal of Human Evolution* 14(3):255–261.

Leighton, M., U. S. Seal, K. Soemarna, Ajisasmito, M. Wijaya, T. Mitra Setia, G. Shapiro, L. Perkins, K. Traylor-Holzer, and R. Tilson. 1995. Orangutan life history and VORTEX analysis. In *The Neglected Ape,* R. D. Nadler, B. F. M. Galdikas, L. K. Heeran, and N. Rosen, eds. Pp. 97–107. New York: Plenum Press.

Lovejoy, C. O. 1981. The origin of man. *Science* 211:341–350.

Medawar, P. B. 1952. *An Unsolved Problem of Biology.* London: H. K. Lewis.

Melnick, D. and G. Hoelzer. 1993. What is MtDNA good for in the study of primate evolution? *Evolutionary Anthropology* 2:2–10. Morin, P. A. 1993. Reproductive strategies in chimpanzees. *Yearbook of Physical Anthropology* 36:179–212.

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

Nishida, T., H. Takasaki, and Y. Takahata. 1990. Demography and reproductive profiles. In *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies,* T. Nishida, ed. Pp. 63–97. Tokyo: University of Tokyo Press.

Obst, E. 1912. Von Mkalama ins Land der Wakindiga. *Mitteilungen der Geographischen Gessellschaft in Hamburg* 26:2–27.

O'Connell, J. F. 1995. Ethnoarchaeology needs a general theory of behavior. *Journal of Archaeological Research* 3:205–255.

O'Connell, J. F., K. Hawkes, N. Blurton Jones. 1999. Grandmothering and the Evolution of *Homo erectus. Journal of Human Evolution* 36:461–485.

Partridge, L., and N. H. Barton. 1993. Optimality, mutation and the evolution of aging. *Nature* 362:305–311.

Pavelka, M. S. M., and L. M. Fedigan. 1991. Menopause: A comparative life history perspective. *Yearbook of Physical Anthropology* 34:13–38.

Peccei, J. S. 1995. The origin and evolution of menopause: The altriciality-lifespan hypothesis. *Ethology and Sociobiology* 16:425–449.

Peters, R. H. 1983. *The Ecological Implications of Body Size.* Cambridge: Cambridge University Press.

Purvis, A., and P. H. Harvey. 1995. Mammalian life-history evolution: A comparative test of Charnov's model. *Journal of Zoology* 237:259–283.

Pusey, A., J. Williams, and J. Goodall. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277:828–831.

Reiss, M. J. 1989. *The Allometry of Growth and Reproduction.* Cambridge: Cambridge University Press.

Rodseth, L., R. W. Wrangham, A. M. Harrigan, and B. B. Smuts. 1991. The human community as primate society. *Current Anthropology* 32:221–254.

Roebroeks, W., N. Conard, and T. van Klofshoten. 1992. Dense forests, cold steppes, and the Palaeolithic settlement of Europe. *Current Anthropology* 33:551–586.

Rogers, A. R. 1993. Why menopause? *Evolutionary Ecology* 7:406–420.

Schultz, A. H. 1969. *The Life of Primates.* New York: Universe Books.

Smith, H., and R. L. Tompkins. 1995. Toward a life history of the Hominidae. *Annual Reviews in Anthropolology* 24:257–279.

Soffer, O. 1992. Social transformations at the Middle to Upper Paleolithic transition: The implications of the European record. In *Continuity or Replacement? Controversies in* Homo sapiens *Evolution,* G. Brauer and F. H. Smith, eds. Pp. 247–259. Rotterdam: Balkema.

Stahl, A. B. 1984. Hominid dietary selection before fire. *Current Anthropology* 25:151–168.

Stanford, C. 1996. The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist* 98:96–113.

———. 1999. *The Hunting Apes.* Princeton; Princeton University Press.

Stewart, K. J., A. H. Harcourt, and D. P. Watts. 1988. Determinants of fertility in wild gorillas and other primates. In *Natural Human Fertility: Social and Biological Determinants,* P. Diggory, M. Potts, and S. Teper, eds. Pp. 22–38. Hampshire: MacMillian Press.

Sugiyama, Y. 1994. Age specific birth rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. *American Journal of Primatology* 32:311–318.

Sugiyama, Y., and J. Koman. 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20:323–339.

Swisher, C. C., G. H. Curtis, T. Jacob, A. Getty, A. Suprijo, Widiasmoro. 1994. Age of the earliest known hominids in Java. *Science* 263:1118–1121.

Tompkins, R. L. 1996. Relative dental development of Upper Pleistocene hominids compared to human population variation. *American Journal of Physical Anthropology* 99:103–116.

Trinkhaus, E., and R. L. Tompkins. 1990. The Neandertal life cycle: The possibility, probability, and perceptibility of contrasts with recent humans. In *Primate Life History and Evolution,* C. J. DeRousseau, ed. Pp. 153–180. Monographs in Primatology, Vol. 14. New York: Wiley-Liss.

Turke, P. W. 1997. Hypothesis: Menopause discourages infanticide and encourages continued investment by agnates. *Evolution and Human Behavior* 18:3–13.

van Schaik, C. P., and J. A. R. M van Hoof. 1996. Toward an understanding of the orangutan's social system. In *Great Ape Societies,* W. McGrew, L. Marchant, and T. Nishida, eds. Pp. 3–16. Cambridge: Cambridge University Press.

Walker, A., and R. Leakey. 1993. *The Nariokotome* Homo erectus *Skeleton.* Cambridge: Harvard University Press.

Wallis, J. 1997. A survey of reproductive parameters in free-ranging chimpanzees of Gombe national park. *Journal of Reproduction and Fertility* 109:297–307.

Washburn, S. L., and C. S. Lancaster. 1968. The evolution of hunting. In *Man the Hunter,* R. B. Lee and I. DeVore, eds. Pp. 293–303. Chicago: Aldine.

Watts, D. P. 1996. Comparative socio-ecology of gorillas. In *Great Ape Societies,* W. McGrew, L. Marchant, and T. Nishida, eds. Pp. 16–28. Cambridge: Cambridge University Press.

Whiten, A., and E. M. Widdowson. 1992. *Foraging Strategies and the Natural Diet of Monkeys, Apes, and Humans.* Oxford: Clarendon Press.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398–411.

Wood, B. and M. Collard 1999a. The human genus. *Science* 284:65–71.

———. 1999b. The changing face of genus *Homo. Evolutionary Anthropology* 8(6):195–207.

Woodburn, J. 1968. An introduction to Hadza ecology. In *Man the Hunter,* R. Lee and I. DeVore, eds. Pp. 49–55. Chicago: Aldine.

Wrangham, R. W. 1987. The significance of African apes for reconstructing human social evolution. In *The Evolution of Human Behavior: Primate Models,* W. G. Kinzey, ed. Pp. 51–71. Albany: State University of New York Press.

Wrangham, R. W. and E. v. Z. Bergmann-Riss. 1990. Rates of predation on mammals by Gombe chimpanzees, 1972–1975. *Primates* 31:157–170.

Wrangham, R. W., and D. Peterson. 1996. *Demonic Males: Apes and the Origins of Human Violence.* New York: Houghton Mifflin.

Wrangham, R. W., C. A. Chapman, A. P. Clarke-Arcadi, and G. Isabirye-Basuta. 1996. Social ecology of Kanyawara chimpanzees: Implications or understanding the costs of great ape groups. In *Great Ape Societies,* W. C. McGrew, L. F. Marchant, and T. Nishida, eds. Pp. 45–57. Cambridge: Cambridge University Press.

Adaptation and Human Behavior

An Anthropological Perspective

Editors

Lee Cronk

Napoleon Chagnon

William Irons

ALDINE DE GRUYTER
NEW YORK

ABOUT THE EDITORS

Lee Cronk is Associate Professor of Anthropology at Rutgers University, New Brunswick, New Jersey.
Napoleon Chagnon is Professor of Anthropology, Emeritus, at the University of California, Santa Barbara, California.
William Irons is Professor of Anthropology at Northwestern University, Evanston, Illinois.

ALDINE DE GRUYTER
A division of Walter de Gruyter, Inc.
200 Saw Mill River Road
Hawthorne, New York 10532

This publication is printed on acid free paper ♾

Library of Congress Cataloging-in-Publication Data
Adaptation and human behavior : an anthropological perspective / [edited by] Lee Cronk, Napoleon Chagnon, and William Irons.
p. cm. — (Evolutionary foundations of human behavior)
Includes bibliographical references.
ISBN 0-202-02043-6 (cl. : alk. paper). — ISBN 0-202-02044-4 (pa. : alk. paper)
1. Sociobiology. 2. Human behavior. 3. Social evolution. 4. Human evolution. 5. Human ecology. I. Cronk, Lee. II. Chagnon, Napoleon A., 1938– . III. Irons, William. IV. Series.
GN365.9.A33 1999
304.5—dc21 99-26821
CIP

Manufactured in the United States of America

10 9 8 7 6 5 4 3 2 1