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From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context

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Abstract

Although humans have a longer period of infant dependency than other hominoids, human infants, in natural fertility societies, are weaned far earlier than any of the great apes: chimps and orangutans wean, on average, at about 5 and 7.7 years, respectively, while humans wean, on average, at about 2.5 years. Assuming that living great apes demonstrate the ancestral weaning pattern, modern humans display a derived pattern that requires explanation, particularly since earlier weaning may result in significant hazards for a child. Clearly, if selection had favored the survival of the child, humans would wean later like other hominoids; selection, then, favored some trait other than the child's survival. It is argued here that our unique pattern of prolonged, early brain growth—the neurological basis for human intellectual ability—cannot be sustained much beyond one year by a human mother's milk alone, and thus early weaning, when accompanied by supplementation with more nutritious adult foods, is vital to the ontogeny of our larger brain, despite the associated dangers. Therefore, the child's intellectual development, rather than its survival, is the primary focus of selection. Consumption of more nutritious foods—derived from animal protein—increased by ca. 2.6 myr ago when a group of early hominins displayed two important behavioral shifts relative to ancestral forms: the recognition that a carcass represented a new and valuable food source—potentially larger than the usual hunted prey—and the use of stone tools to improve access to that food source. The shift in the hominin "prey image" to the carcass and the use of tools for butchery increased the amount of protein and calories available, irrespective of the local landscape. However, this shift brought hominins into competition with carnivores, increasing mortality among young adults and necessitating a number of social responses, such as alloparenting. The increased acquisition of meat ca. 2.6 Ma had significant effects on the later course of human evolution and may have initiated the origin of the genus *Homo*.

Keywords: Life history; breastfeeding; hominin diet; *Homo*

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Introduction

All mammals face a reproductive dilemma: the intense energetic demands of lactation delays a mother's future reproduction, yet weaning a nursing infant too soon places it at a variety of risks, including increased mortality and morbidity from infectious and parasitic diseases that potentially restrict growth and development. The balancing act between these reproductive decisions helps determine population growth, individual growth rates, lifetime female fertility, and influences a number of other life history parameters.

The great apes nurse long and wean late (*Pan troglodytes* weans, on average, ca. 5 years [Clark, 1977]; *Pongo pygmaeus* at 7.7 years, possibly the latest of any mammal [Galdikas and Wood, 1990]), improving the survival potential of juvenile individuals, but restricting future population growth. Hence, the ape's dilemma described by Lovejoy (1981). This late weaning explains, in part, why some hominoid species are in decline (e.g., *Gorilla gorilla beringei* [Fossey, 1983], *Pongo pygmaeus* [Galdikas and Wood, 1990], and *Pan paniscus* [DeWaal, 1982]), while others show virtually no population growth (*Pan troglodytes* [Teleki et al., 1976; Nishida, 1990]). Modern humans that live in traditional, natural fertility societies, on the other hand, generally wean between 2-3 years (see below and Table 1), increasing the risks to the child and creating the weanling's dilemma (e.g., Martines et al., 1994), but increasing the possibility of population growth. While the current disparity between ape and human population growth is due to a number of factors (e.g., habitat destruction, human hunting, and technological advances), the apparently derived human pattern of early weaning, relative to other hominoids, requires explanation. If selection had targeted only the survival of the child, we would wean late, as the apes do. If not the child's survival, what, then, has selection targeted in humans? The purpose of this paper is to explore why and how selection has proceeded in this unexpected direction.

Hominoid reproduction

All hominoids, human and non-human alike, share many features of their reproductive physiology. In comparison with most other mammals, for example, all hominoids grow slowly and reach reproductive age relatively late in life, and parental investment in individual offspring is high, resulting in relatively few births per female. Such a pattern of delayed development and low fecundity was initially explained by ecologists as a typical life history pattern of social mammals living in a stable environment with predictable resources; under such conditions, it was argued, population size generally remains stable, near carrying capacity, and shows little longitudinal increase (e.g., MacArthur and Wilson, 1967; Pianka, 1970). Ross (1988) confirmed that primates living in (presumably predictable) tropical rain forests have slower development (when effects of body size are controlled for) than primates living in (presumably less predictable) savannas and secondary forests. Although Harvey et al. (1989) later argued that environmental "harshness," associated with increased levels of mortality, was a more critical ecological variable than "predictability," they nevertheless again confirmed a connection between ecology and certain life history variables, while revealing the value of age-specific mortality patterns in determining reproductive rates. Other work, however, has revealed the complexity of the relationships between environment and life history variables (see Ross and Jones, 1999). Some writers, noting that slow growth generally leads to larger adult body size, have stressed the importance of size in resisting environmental hazards such as predation (e.g., Pianka, 1970; Western, 1979; Clutton-Brock and Harvey, 1983); slow growth, moreover, enhances the development of social and extractive skills, which, in turn, enhance survival (e.g., Pagel and Harvey, 1993). Many workers, in fact, have argued that, for social species, such as most anthropoid primates, there are important adaptive advantages to prolonged development because it provides ample time to develop both the social skills necessary to survive in a complex, hierarchical group and the cognitive skills necessary to exploit embedded or protected resources. Females, moreover, would have time to develop the parental skills that will later optimize the survival of their own young (e.g., Lancaster and Lancaster, 1983; Jolly, 1985; Ross and Jones, 1999). Joffee

Table 1
Age at weaning in natural fertility populations

Species	Weaning (in months)	References
Homo sapiens		
Africa		
Algeria	14.4	eHRAF
Amhara	24	eHRAF
Azande	24-36	eHRAF
Bambara	30	eHRAF
Bemba	24-36	eHRAF
Burundi	24	eHRAF
Dogon	24	eHRAF
Gambia	21	Fildes, 1986
Ganda	36	Mair, 1940
Hadza	45.1	Kaplan et al., 2000
Hausa	24	Kaplan et al., 2000
Igbo	24-26	Kaplan et al., 2000
Inesis	23.2	eHRAF
Ivory Coast	42	eHRAF
!Kung	49	Howell, 1999
Masai	36	Howell, 1999
Nigeria	21	eHRAF
Nuer	14-24	eHRAF
Ovimbundo	24	eHRAF
Sine	24.3	eHRAF
Somalia	24	eHRAF
Tiv	24	eHRAF
Ubena	24-36	eHRAF
Wolo	18-24	eHRAF
Asia		
Bengali	24-36	eHRAF
Kanuri	18	eHRAF
Lepchus	24-36	eHRAF
Sanlei	24	eHRAF
Thai (Central)	24-36	eHRAF
South America		
Ache	25	Hill and Hurtado, 1996
Aymara	12-24	eHRAF
Hiwi	45.1	Kaplan et al., 2000
Tarahumara	36-48	eHRAF
Warao	24	eHRAF
Yanomano	34.4	Melancon, 1982 (cited in Hill and Hurtado, 1996)
Meso-America		
Kogicol	12	eHRAF
Maya	18-24	eHRAF
North America		
Delaware	36-48	eHRAF
Inuit	36-48	eHRAF
Ijibwa	24-36	eHRAF
Iroquois	24-30	eHRAF
Yokut	24	eHRAF
Pacific Islands		
Amele	36	Worthman, et al., 1993
Fiji	12	eHRAF
Gainj, New Guinea	43.3	Galdikas and Wood, 1990
Trobriand Is.	24	eHRAF
Pan troglodytes	48-54	Goodall, 1989
	67	Clark, 1977
Gorilla gorilla berengei	42-54	Fossey, 1979
	42-54	Schaller, 1963
Pongo pygmaeus	92.6	Galdikas and Wood, 1990

(1997) focused this argument on the importance of social pressures by demonstrating a positive correlation between brain size (particularly the non-visual neocortex) and the length of the juvenile period. Charnov, on the other hand, emphasized the role of mortality in determining both age at first reproduction and total lifespan since the prolonged period of juvenile growth in primates would necessarily result in higher rates of pre-reproductive mortality (Charnov and Berrigan, 1993; Charnov, 1993). Delayed reproduction would, therefore, be expected to be associated with relatively low adult mortality and a long lifespan. Charnov's (1993) perspective is interesting because he argued that slow growth may reflect, in part, a cost, rather than a benefit, of growing a large brain. Others, such as Janson and van Schaik (1993) have also emphasized the vulnerability of slow-growing subadults, arguing that such slow growth may reduce the chance of starvation (by reducing energetic needs) while providing ample time to learn to avoid predators and environmental hazards. Therefore, the developmental and mortality patterns that characterize the hominoids may have a variety of social and ecological explanations. This issue will be revisited at the conclusion of this paper.

Whatever the explanation of the pattern, the reproductive success (RS) of any female mammalian cohort, assuming pregnancies with a single neonate, is due to a combination of age at sexual maturity, the length of the reproductive span, and the interval between births and can be represented very simply as:

$$RS = \frac{MLS - s}{IBI}$$

where MLS = maximum female lifespan, s = age at first birth, and IBI = inter-birth interval (adapted from Wilson, 1975).

Each of these variables is determined by a number of factors. A female's age at first birth, for example, is determined largely by a species' physiology. Most species show minimal intraspecific variability in age at first birth (Harvey and Clutton-Brock, 1985). Nevertheless, it has been pointed out that in modern women, average age at menarche may be either delayed or advanced by an individual's energy balance and nutritional status (Ellison, 1990; Jasienska, 2001), a finding that may be extended to other mammals (Lee et al., 1991). While a female's age at first birth generally varies relatively little within a species, her lifespan and the inter-birth interval are more sensitive to environmental and behavioral factors and show considerably more variation.

The probability of a female's survival to the end of her predicted lifespan is a combination of heritability and stochastic variables, such as hazards (toxic foods and injuries), disease, and resource reliability. Female survival has no predictable or consistent relationship with any particular ecological or behavioral variable (Harvey and Clutton-Brock, 1985; Lee et al., 1991), although in highly socialized mammals, like the hominoids, it may be mitigated to some degree by coordinated group actions and learned, individual responses. Since female fertility declines with age, an extension of average lifespan (beyond ca. 40 in humans) will have little effect on her completed fertility. The contribution of post-menopausal females to her kin's fertility (the "grandmother hypothesis") is currently the subject of some controversy. O'Connell et al. (1999) argued that post-menopausal females were of critical importance in the early stages of hominin evolution, while Kennedy (2003) and Kurland and Sparks (2003) noted that the fossil and archaeological records, while imperfect, contain no evidence that older individuals, of either sex, survived in sufficient numbers to provide significant aid in either child care or subsistence activities.

The interval between births (IBI) is the most complex variable of all, and reflects a mother's biological imperative to direct her metabolism and nutritional stores toward the support of herself and an existing infant over that of a developing fetus. Without doubt, the most important contributor to the IBI is the lactational suppression of ovulation, largely through the mechanism of nipple stimulation. Such anovulation is achieved primarily through the release of hypothalamus (gonadotropin-releasing hormone, or GnRH) and pituitary (prolactin) products that suppress ovulation (e.g., Taylor et al., 1999). Therefore, "lactational sterility" is largely a function of the frequency of nursing (Konner and Worthman, 1984; Lunn et al., 1984; Ellison, 1990) rather than the amount of milk produced. For example, !Kung mothers, who nurse their infants on demand an average of four times an hour (Konner and Worthman, 1980), will have higher levels of prolactin and ovarian steroids and, as a result, more complete lactational anoestrus than will Bakuvu women, who nurse just 4 to 6 times a day (Delvoye et al., 1977) and who may resume cycling while still lactating.

Although nursing itself is the most important contributor to lactational anoestrus, the IBI may be influenced by other factors as well. A mother's age and parity may increase the IBI: older females and those with high parity will experience more cycles before reconception (Henry, 1961) than younger women and/or those who have had fewer births (Galdikas and Wood, 1990; Bowman and Lee, 1995). On the other hand, the presence of significant paternal provisioning (Galdikas and Wood, 1990) or the death of a nursing infant may shorten the interval. Just as energy balance and nutritional status may affect age at menarche, such factors may also shorten or lengthen the IBI. For example, the Amele of New Guinea practice a pattern of frequent and extended nursing and yet have a high birth rate (mean lifetime fertility = 6.8) relative to most other natural fertility populations; the rapid return of ovulation while they are still lactating may demonstrate the effects of a relatively light work load and a high nutritional status (Worthman et al., 1993).

Weaning age, because of its strong determinative relationship with maternal fertility, has been occasionally used as a proxy for the interbirth interval: "we have [defined weaning age in primates and elephants] as the average age of the offspring when reconception took place" (Lee et al., 1991:101), rather than the more conventional definition of "cessation of suckling." Although data for both "weaning" (as "cessation of suckling") and observed IBI are available for very few societies, the data that are available appear to suggest that the two variables may not, in fact, be equivalent in humans. Among the Ache, for example, weaning occurs, on average, at 25 months, when a woman is generally already two or three months pregnant, yet the mean IBI for the Ache is 37.6 months (Hill and Hurtado, 1996: 221, 262). Using the definition of Lee et al., the weaning age/IBI of the Ache would be predicted to be 22-23 months. In the Amele, the situation is reversed: they wean, on average, at 36 months, yet have an IBI of 28 months (Worthman et al., 1993), indicating that in humans, a woman may nurse infants of different ages, a situation that has not been reported for the apes. While IBI and weaning age may, indeed, be equivalent in non-human hominoids, as Lee et al. claim, the timing of reconception is likely to be a far more complex variable in humans than it is in non-human hominoids, mediated by factors such as infanticide, coital taboos, disease (particularly STDs), and nutritional status, which are either relatively unimportant or do not occur in other animals.

Weaning age: predictions

There is a considerable literature on the factors that may predict the "natural" weaning age in modern humans living in traditional societies. Such societies, by definition, would not use proprietary contraceptives or manufactured infant foods (see review in Dettwyler, 1995). Harvey and Clutton-Brock (1985), for example, proposed an allometric effect on weaning time based on their finding of a high positive correlation between weaning age and maternal weight ($r = 0.91$). Thus, they propose that weaning age (in days) $=$ $2.71 \times$ adult female body weight (in grams)$^{0.56}$; this relationship predicts an average weaning age for modern humans of 3.36 years (range 2.8-3.7 years). Charnov and Berrigan (1993), on the other hand, stated that weaning should occur when the infant reaches about 33% of adult body weight, predicting weaning ages for well-nourished western children of 5.75 years for girls and 7 years for boys. Smith (1992) found a very high correlation between weaning age and the timing of the eruption of M_1 ($r = 0.93$; slope $= 1.07$), a relationship so close she termed it "isochronous." This would predict a weaning age of 5.5 to 6 years in humans, the age, she claims, at which a youngster can effectively acquire and process an adult diet (Smith, 1992; see also Smith et al., 1994). Still others have argued that weaning occurs at some multiple of neonatal birth weight. Lawrence (1994), for example, in a textbook that is frequently cited and used by medical professionals, argued that an infant should be weaned when it has tripled its birth weight; in well-nourished western infants, this occurs, on average, at about 9 months. Others have proposed 4:1 as the appropriate relationship between weaning and birth weights, arguing that when an infant has quadrupled its birth weight, the mother's metabolism can no longer support the energetic needs of her infant (Lee et al., 1991; Bowman and Lee, 1995). These authors predicted that in "food-limited" societies, human weaning age should be ca. 36 months. Others have argued that weaning age may reflect, in part, the availability of appropriate weaning foods (Galdikas and Wood, 1990) or social factors, such as the presence of effective paternal provisioning to help support the weanling's needs (Lovejoy, 1981; Galdikas and Wood, 1990). Thus, the range of predicted weaning ages for modern humans varies from a minimum of nine months, using gestation length or 3:1 weaning/neonate weight, to more than 7 years, using adult body weight$^{0.33}$. The very wide range of these predictions, despite their firm mathematical basis, suggests that the factors involved in determining the termination of lactation, in humans at least, are not well understood.

For that reason, an investigation into observed weaning time in ape and human populations seems timely.

Weaning age: observed

Weaning is a process, not an event that can be placed at a specific point in time; therefore, it is not subject, in any meaningful way, to precise mathematical or statistical analyses or even to exact determination. Sellen's (2001) recent paper has, perhaps, done as much as possible to overcome the inherent problems of determining human weaning time. An "average" age of weaning can only suggest the age at which most young in a particular group cease nursing; moreover, in humans, as the Amele demonstrate, it is not uncommon for a mother to continue to nurse an older youngster even though she has an infant as well. Data reported in Table 1 were taken from field studies, individual ethnographic reports, and from the Human Relations Area Files (HRAF: category 862, on-line edition); data points were included only when a definite age or clear range was expressed. All were pre-industrial, "natural fertility" populations practicing a range of subsistence economies from agriculture to foraging, and many were mixed economies. It has been suggested that weaning time in human societies should vary in a consistent way with subsistence practices and with the availability of appropriate weaning foods (e.g., Flannery, 1973; Larsen, 1995). Thus, agriculturalists and pastoralists should, in theory, wean earlier than foragers. A recent study found that, in general, this is true: foragers wean later, and agriculturalists wean somewhat earlier (Sellen and Smay, 2000). The differences between the groups, however, are not pronounced and foragers did not, in fact, lack weaning foods. For this reason, the societies included here were not separated according to their subsistence practices. In addition, field studies of weaning time in ape and human societies (see Table 1) have been carried out by many different scholars, with a wide range of backgrounds and training, and their reports of weaning time show no common methodology or definitions. The frequency in Table 1 of phrases such as "24 months" or "36 months," particularly in the human data, demonstrates the crudeness of the scale used. Finally, there have been only a limited number of field observations on the nursing behavior of the great apes; inclusion of studies of captive animals would have increased the sample size but such studies of provisioned, predator-free groups would seem to have little relevance for questions of evolutionary development. Moreover, studies of captive chimps (Courtenay, 1987) and orangutans (Markham, 1995) generally show earlier weaning and shorter IBIs than comparable wild groups; this is not true, however, of captive gorillas (Sievert et al., 1991), which show little distinction from their wild counterparts in these reproductive data (see also Knott, 2001). While not included here, captive studies are nonetheless valuable in demonstrating the inherent variability of weaning time and its responsiveness to activity levels, risk factors, food supply, and even social rank (see Pusey et al., 1997; Wallis, 1997; Knott, 2001). While these caveats are important and must be considered in any later conclusions, a clear pattern, nevertheless, emerges from the available studies.

Results

If the hypothesis is correct that slow growth and long-term infant dependency reflect a need to acquire social and cognitive skills, then the nursing period should reach its maximum among modern humans, who grow more slowly and reach reproductive age later than other primates (Schultz, 1960; Martin, 1983). Other hominoids should, therefore, demonstrate absolutely earlier weaning (for a recent example of such an assumption, see Vasey and Walker, 2001).

The great apes

The most detailed study of nursing behavior among the great apes was carried out on *Pan troglodytes* by Clark (1977) at Gombe. She reported that suckling lasted, on average, 62.8 months, with a range of 52 to 86 months, resulting in an IBI of ca. 5 years. In fact, during the study period, there was no birth at Gombe until the mother's existing infant had reached at least 4 years of age (Clark, 1977). Interestingly, as weaning time approached, both the length of suckling bouts and their frequency increased (at age 25-30 months: 1x/hr.; at 30-36 months: 1.3 x/hr.), suggesting the stressfulness of the weaning process. Other field studies on *P. troglodytes* that have reported the IBI rather than weaning time (as cessation of nursing) have confirmed Clark's findings, with a minimum of 5.0 years at Boussou (Sugiyama, 1994) and a maximum of 6 years at both Mahale and Kanyawara (Nishida et al., 1992; and Wrangham, in Knott, 2001).

Chimps at Gombe have a mean total reproductive span of ca. 25 years (first birth, 13-14 years; last birth ca. 40 years; Teleki et al., 1976), resulting in an average of 5 births per female. However, infant mortality is high. During a ten-year study at Gombe, slightly more than half of all deaths occurred prior to adulthood (51.5%; Teleki et al., 1976: 569), clearly illustrating the ape's dilemma: despite intense, long term maternal care, more than half of all chimp infants did not survive long enough to reproduce, effectively limiting population growth. Animals that do reach reproductive age, however, are likely to do so successfully and repeatedly, albeit slowly.

Although field data for other great apes provides less fine-grained detail than Clark's (1977) study, a similar pattern of prolonged nursing and a long IBI is apparent. Field studies of *P. paniscus* are limited, but Takahata et al. (1996) reported that the IBI at Wamba occurred at 54 months, whereas Kano (1992: 77) reported that a mean IBI of 5 years for this species was probably too low. Schaller (1963) and Fossey (1983) reported that *Gorilla gorilla beringei* wean between 3.5 to 4.5 years, and Watts (1991) reported an IBI of 3.9 years at Karisoke. Reproductive rates are extraordinarily long for *Pongo pygmaeus*: Galdikas and Wood (1990) report that, at Tanjung Putting, they found a mean weaning age of 7.7 years, while at Ketambe the IBI was reported as 8.4 years (Utami, in Knott, 2001).

Homo sapiens: modern populations

In a widely cited monograph on human reproduction, Ford (1945:84) stated that, based on his study of the HRAF, weaning in "traditional" societies occurred "at about three years," but provided no actual data. A review of the HRAF (on-line edition), however, showed that weaning age was seldom expressed with even the qualified certainty suggested by that statement. Among the Hopi, for example, "a child is nursed [to] the age of 2 and 3 or 4 years," while the Ojibwa generally wean "at 2 years but it is not uncommon for a woman to nurse two infants, the oldest being 3-4 years old." Although Ford's weaning age of "three years" has been repeated by others (e.g., Dettwyler, 1995), it is not entirely accurate. Although a mean weaning age can be calculated from the human data in Table 1 (30.1 months; n = 46), it seems more accurate to conclude that the "natural" weaning age for humans is between 2-3 years and generally occurs about midway in that range. The minimum reported weaning age was one year (Fiji, Kogicol) and the maximum was about 4 years (several native American groups); several entries, however, reported that individual children may nurse as long as 6 years. Goodall (1986) also reported that a few Gombe chimps also nursed far longer than the population average. Sellen (2001), using a slightly larger sample (n = 113) also taken from the HRAF (microfiche edition), reported a very similar mean (29 months ± 10 months), and a very similar peak weaning period between 2 and 3 years.

Homo sapiens: ancient populations

Other data, for ancient populations, appear to confirm a "natural" weaning age between 2 and 3 years. For example, Fildes' (1986) study of ancient texts, such as the Bible (Macabees 7:27), the Koran, Egyptian medical papyri, and Babylonian cuneiform documents, reveals a frequent admonition to wean by about 3 years; the Talmud, however, suggests 24 months. As noted below, stable nitrogen isotope analysis on bone tissue from several prehistoric societies suggests a somewhat wider range of "natural" weaning ages. For example, since nursing infants occupy a different (higher) trophic level than do their mothers, the isotopic composition of nursing infants' bones and teeth should, in theory, differ from that of the adults in their group. Weaning time, therefore, should correspond to the point at which infant and adult tissues reach a similar isotopic composition (Herring et al., 1998). Following Fogel et al. (1989), several authors have found an elevated level of $\delta^{15}N$ in infant osteological remains (relative to adults of the same group), which, they argued, constitutes a "nursing signal" (Katzenberg, 1992; Katzenberg et al., 1993, 1996; Schurr, 1994; Tuross and Fogel, 1994; White and Schwarcz, 1994). For example, at the Sully site in North Dakota and at the Angel site in the Ohio Valley, $\delta^{15}N$ reached adult levels at about 24 months (Tuross and Fogel, 1994; Schurr, 1997), suggesting rather early weaning. In Nubia, on the other hand, there was a gradual decline up to about age 6, indicating a slow introduction of adult foods (White and Schwarcz, 1994). Others have used stable carbon and oxygen isotopes in dental enamel to track dietary changes in young children. Stable carbon ($\delta^{13}C$), for example, may be used to detect the introduction of solid foods, and hence the beginning of the weaning period, while oxygen isotopes ($\delta^{18}O$) may track the decreasing consumption of human milk (Wright and Schwarcz, 1998). Using this approach, it was found that, among the Preclassic and Postclassic Maya, solid foods were first introduced probably late in the first year, but that the weaning process was not concluded until 5 or 6 years (Wright and Schwarcz, 1998). Thus, extensive field data, collected in modern traditional societies, ancient textual references, and biochemical evidence from prehistoric societies, all suggest that in humans, the "natural" weaning age is generally between 2 and 3 years, although it may continue longer in some groups.

Thus, the differences between the predicted and observed weaning time in humans is considerable, a fact also noted by Sellen (2001), indicating that the factors that determine weaning age in humans are not well understood. Although some authors have found very high correlations ($r \geq 0.90$) between weaning age and certain variables, those variables (maternal weight: Harvey and Clutton-Brock, 1985; eruption of M1: Smith, 1992) may, in fact, play only an indirect role in weaning time and, as a result, have no predictive value. This would seem to confirm Horn's (1978) rather acerbic comment about the "turgid mathematical formalism" of life-history predictions in general. None of the predictions, in fact, reflected the finding of an average weaning age of 30 months. The closest was that of Lee et al. (1991) at 36 months. Clearly, there is a danger in making life history predictions when the actual relationships of the included variables are poorly understood.

While concerns about habitat disturbance and the possible effects of observer interference (e.g., provisioning) must not be overlooked, the evidence of a longer nursing period in the great apes relative to modern humans in traditional societies is clear. Moreover, ancient texts and isotopic data indicate that this may be a long-term characteristic of *Homo sapiens*, a claim that requires further verification. Clearly, the search for a "weaning signal" in bone or dental tissue from pre-*H. sapiens* hominins would be of great interest.

The demographic effects of the differences in weaning age between apes and humans are readily apparent: a chimp will have her first birth between 13 and 14 years, while an Ache woman will have her first birth somewhat later, at about 19.5 years; both will have their last birth at ca. 37 years (see refs. in Table 1). Thus, chimps have, on average, a somewhat longer total reproductive period than an Ache woman, but a female chimp, because of prolonged nursing and the length of her IBI, will have, on average only 5 births during her lifetime, whereas, an Ache woman's completed fertility will be slightly more than 7 births. Therefore, even if human pre-reproductive mortality remains as it is in the great apes (i.e., between 50% and 60%), the shorter human nursing period and IBI yield a potential for population growth. If neonate and weanling survival improved (see below), the possibility for population growth would equally improve.

The weanling's dilemma

Weaning late, as non-human hominoids do, may enhance the survival of individual youngsters, but it limits population growth; weaning earlier, as modern humans do, may help to solve that problem, but brings with it other difficulties and hazards, exchanging the ape's dilemma for the weanling's dilemma (e.g., Martines et al., 1994). For example, the mammalian immune system matures rather slowly in the post-natal period, giving the infant a limited ability to respond to many infectious assaults; milk, however, possesses a number of factors that provide "passive immunity," but, obviously, will be lost at weaning. Passive immunity, through the actions of lymphocytes, macrophages, interferon, and particularly the secretory immunoglobulins (S Ig), provides protection to a wide variety of food-borne and contagious-disease-causing viral and bacterial pathogens. While the infant can produce adult levels of S Ig G by 36 months (Hayward, 1986: 383), for example, other components of the immune system do not develop until much later: the production of the important S Ig A, for example, does not reach full maturity until age 12 (Hayward, 1986). In addition, slow dental development limits the weanling child's ability to process an adult diet efficiently. In modern humans, the adult dentition does not begin to appear until 5.5 to 6 years (Smith, 1991); therefore, between the ages of 24 months (when the full deciduous dentition is in place) and about 6 years, the child must depend on the primary teeth, which have thin enamel and short roots in comparison to the adult dentition and are, therefore, more liable to wear, breakage, and loss during mastication of tough, coarse, or gritty foods. This problem may become particularly severe between the ages of 4 and 6, when the primary teeth have become worn, but nutritional demands are high because of growth (see below). Although specific ontogenetic data are limited, digestive immaturity also restricts, to some degree, a weanling's ability to process adult foods. A small stomach and short intestinal tract (particularly the small intestine, where most absorption occurs) relative to the adult condition means that the child will have a limited ability to extract nutrition from the food consumed (Bailey et al., 1984). Finally, the youngster's small size, relative to adults, renders him or her an ineffective competitor who faces obvious difficulties, first, in acquiring foods that may be nutritious but well protected (e.g., large nuts, meat, marrow, and brain tissue) or deeply embedded USOs (underground storage organs, such as roots and tubers) and second, once acquired, they may have difficulty in preparing or retaining such foods long enough to consume them.

However, supplementation, which, according to the HRAF, generally begins in traditional societies in the second half of the first year, carries its own dilemma: while such foods are necessary to augment maternal lactation, they can act as a route for the introduction of intestinal parasites and food-borne pathogens. In one study, even with the provision of significant supplementation (22 g of protein and 200 calories per day), recurrent diarrhea "substantially" interfered with normal rates of growth and development (Mora et al., 1981: 1885). Thus, in combination, nutritional limitations imposed by the deciduous dentition and the immaturity of both the immune system and the digestive tract renders the weanling child especially vulnerable to increased morbidity from infectious and parasitic diseases, delayed or reduced growth, and higher mortality (e.g., Katzenberg et al., 1996) relative to well-nourished children. Moreover, studies in Thailand (Bailey et al., 1984), Colombia (Mora et al., 1981), and Guatemala (Behar, 1977) have indicated that such disorders are not due to the deficiency of any particular nutrient, but are due to overall protein/calorie insufficiency.

Obviously, parental attention and food preparation (e.g., tools, cooking) will offset some of these difficulties, but no amount of care or cultural management can compensate for the danger of intestinal parasites or infectious disease related to an immature immune system, the inability to digest adult foods efficiently, or the long term developmental deficits that can emerge from chronic nutrient insufficiency. As Lee et al. (1991) have shown, weaning age is a complex variable, but, in any case, it would seem highly advantageous for humans to continue nursing, as many mammals do, until the child's size, dentition, digestive tract, and immune system are mature enough to provide him or her with an optimum opportunity to survive. But human children are weaned long before a number of important developmental milestones are reached. Why, then, are human children weaned so early in the face of so many threats to their life and development? The answer, in part at least, appears to be quite straightforward.

Adolph Schultz's (1960) graphic depiction of the comparative life histories of primates, shown in Fig. 1, has been frequently reproduced; it fails, however, to reveal a very important and critical difference between ape and human growth. Schultz used the timing of the eruption of the adult dentition to gauge the timing of major life history events, and the diagram implies that all body systems (dental, skeletal, reproductive, and the central nervous systems—including the brain) reach maturity at about the same time (or that any differences in their development are unimportant). This is not, in fact, true. While the skeleton, dentition, and reproductive systems do complete most of their growth at approximately the same age in modern humans (12 years, on average, for modern females; 18 years for males), the human brain grows much faster and completes its growth far earlier than other systems, achieving nearly 100% of its adult weight by about age 7 (Cabana et al., 1993). Here lies the important difference between ape and human growth.

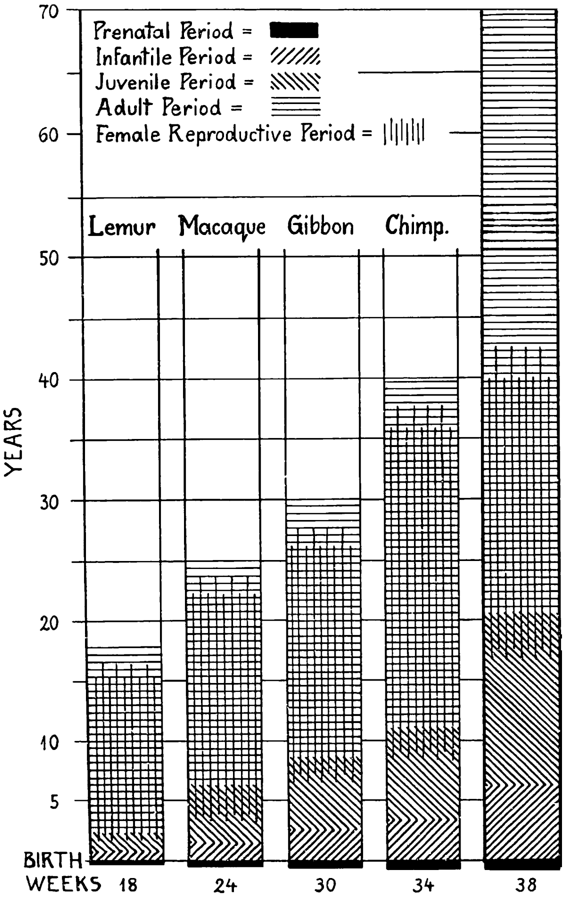

Fig. 1. Comparative life histories of primates. Schultz's (1960) well known diagram suggests that all systems (dental, reproductive, skeletal, and central nervous system/brain) mature at approximately the same time. While the dental, reproductive, and skeletal systems do reach maturity at similar times, the modern human brain matures far earlier, reaching adult volume by about age 7.

At birth, chimps and humans both have brain weights that are, on average, about 1/3 of their adult size (*Pan*: 128/410 ml; *H. sapiens*: 384/1250 ml; Harvey and Clutton-Brock, 1985). However, in terms of absolute size, the chimp neonate brain will need to grow less than 300 ml more to reach adult volume, while the human brain will need to grow nearly 900 ml. Since chimps and humans both attain adult brain size between 6 and 7 years (Keith, 1895; Zuckerman, 1928; Cabana et al., 1993), the human brain, as Martin (1983) has shown, retains a rapid, altricial-like pattern of growth throughout the first year, leading to Portmann's (1941) suggestion that humans are "secondarily altricial." In developmental terms, modern humans achieve adult brain size (by weight) soon after the eruption of M1, while in *Pan*, adult brain size is reached at a more advanced developmental stage, with the eruption of M2 (Keith, 1895; Zuckerman, 1928), although absolute age is very similar. In modern humans, then, the period prior to 7 years is critical for brain growth and, therefore, for the child's intellectual potential.

The brain is a very "expensive" organ, with adult humans requiring about 20-25% of their total BMR (basal metabolic rate) to maintain it (Aiello and Wheeler, 1995). It is even more expensive for human children, whose brains require metabolic energy not only for maintenance, but for growth as well, and who, as a result, must devote as much as 80% of their resting BMR to the brain (Leonard and Robertson, 2002). The dietary support for such elevated rates of metabolic activity is reflected in a child's elevated need for many nutrients, particularly in an increased need for protein and calories. A three year old child, with a body weight of ca. 13 kg, requires about 14.3 g of protein daily (1.1 g/kg/day) to support optimal health and development (Dietary Reference Intake, 2002); at age four, with a body weight of ca. 20 kg, the daily protein requirement jumps to 19 g, even though the per-unit-weight requirement has dropped slightly (0.95 g/kg/day; Dietary Reference Intake, 2002); the need for other nutrients, particularly calories and the water soluble B vitamins, is similarly elevated at this time. However, maternal lactational output has limits. Authorities generally agree that a well-nourished, average size woman nursing a single infant can produce a maximum of about 1200 ml of milk per day (Hambreaus, 1977); the world-wide average for "mature" milk production is actually somewhat less, between 700-800 ml milk per day (WHO, 1985). Human milk, relative to cow's milk, however, is low in protein (related, perhaps, to our slow growth; Oftedal, 1984), containing about 0.95 g of protein per 100 ml of milk (WHO, 1985). Therefore, at maximum levels of production, a - modern, well-nourished woman nursing a three year old child can produce about 80% (11.4 g) of the protein her child needs. However, with more realistic levels of production (700-800 ml per day), i.e., those found in women whose own nutritional status may be less than optimum, her milk will satisfy only about 50% of those protein needs. (Maternal nutritional status may affect the volume of milk produced, but not its protein/calorie content.) By age 4, the protein deficit may become substantial: at maximum levels of production, a woman can produce only about 50% the protein her child needs, but with average production, she can produce only about 33% of those needs.

Thus, after approximately age 3, a growing child's daily protein deficit would become substantial and would increase rapidly in the presence of a significant parasite load or chronic infection and/or the absence of highly efficient weanling foods, resulting in a potentially significant impairment of growth and development and increased levels of morbidity and mortality. Fig. 2 shows that the child's need for calories is similarly elevated beyond maternal capacity by 3 years of age. This, in short, explains why the natural age of human weaning is between 2 and 3 years: it is not a choice, but an imperative, directly related to the human child's large and rapidly growing brain. Clearly, early weaning and the large brain in modern humans are not only interrelated, they are interdependent, with the early shift to adult foods being necessary to support the human brain's increased metabolic needs despite the associated dangers.

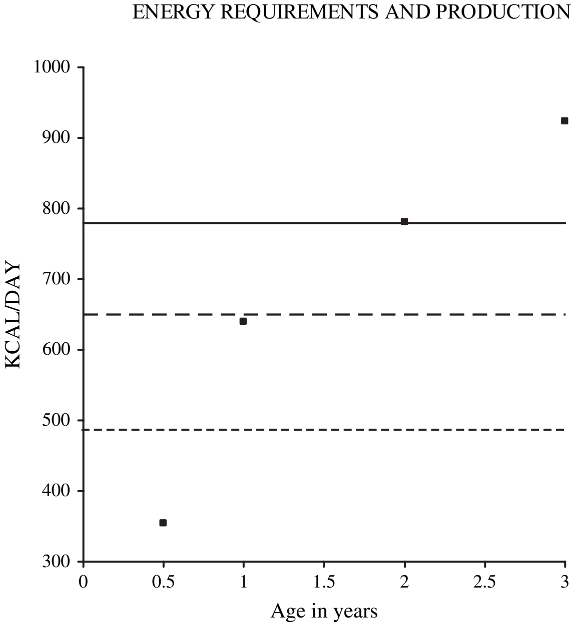

Fig. 2. Infant energy requirements and mother milk production capacity. Solid squares indicate an infant's caloric needs at a particular age; dotted line indicates average milk production of a lactating mother, while the dashed and solid lines indicate heavy and maximum milk production levels, respectively. While a mother's lactational production (by volume) remains relatively stable at average, heavy, or maximum levels through time, her infant's needs increase. At average levels of milk production (750 ml/day), a woman can produce 487 kcal/day (65 kcal/100 ml; Lawrence, 1994); at 1,000 ml of production, she produces 650 kcal/day, easily sufficient in the first 6 months of life (requirements: 71 kcal/kg; Lawrence, 1994). By one year, with a 9 kg infant (now requiring 639 kcal/day), her ability to produce calories begins to fall behind her infant's needs, explaining why supplementation generally begins in the second half of the first year. At two years, an 11 kg child requires roughly 781 kcal/day; at three years, a 13 kg child requires 923 kcal/day. Long term lactation, even at "average" levels of production, represents a challenge to a woman's energetic, nutritional, and reproductive status. Maintaining lactation at above-average levels of production much beyond one year could represent a significant challenge to her status.

This prolonged and rapid, yet early, period of human brain growth may be important in other ways. Most mammals, in fact, move rather quickly from weaning to the more independent juvenile period (Pagel and Harvey, 1993); only humans extend this vulnerable period of development. Bogin (1997) argued that the period between 3 and 7, which he calls "childhood," is unique to humans and has described a number of social and cognitive reasons for extending this period (Bogin, 1997, 1999a,b). One further reason, perhaps, should be added to his discussion.

The adult mammalian brain is the result of both genetic and epigenetic factors. In humans, the production of neurons is largely completed before birth followed in the post-natal period by the development of associated glia, synapses, and axons. Both processes are largely under genetic control (Huttenlocher, 1979; Rapoport, 1999). In humans between the ages of 3 and 7, there is an "exuberant over-production" of glia, synapses, and axons that reaches a peak about age 5; at that age, in the mid-frontal cortex, for example, synaptic density reaches $17.5/\text{mm}^3 \times 10^8$, but in the adult, this density will be, on average, just $10/\text{mm}^3 \times 10^8$, a 57% reduction (Huttenlocher, 1979, 1990). This loss of synapses, or "apoptosis," reflects the brain's "neuroplasticity": neurological connections that are activated before growth is completed will remain active in adulthood, while those not activated will be pruned and lost (Huttenlocher, 1979, 1990; Rapoport, 1999). Thus, early establishment of synapses and activation of glia and neuronal connections can permanently modify the structure of the brain (Zilles, 1992; Thoenen, 1995; Rapoport, 1999), thereby improving its potential. Laboratory data have long shown that environmental complexity can have a positive and direct effect on brain structure (Bennett et al., 1964; Somers et al., 1999; Wolffe and Matzke, 1999; Rampon et al., 2000), and it may be that the less unpredictable, vicariant habitats that first emerged ca. 2.5 Ma (Vrba, 1992) established a new selective background favoring individuals who were particularly capable of flexible or inventive responses to novel stimuli.

In the terminology of developmental psychology, the period of glial and synaptic over-production represents the "pre-operational" stage. It is during this period that some aspects of the child's learning potential, including its potential for language acquisition, are at their height. After the pruning period, the child's thinking processes are more controlled and focused, indicating that the transition to the "concrete-operational" phase has occurred (Piaget and Inhelder, 1969). Anthropologists have termed this the "5 to 7 shift" (e.g., Weisner, 1996; see below). Thus, although this prolonged period of development—i.e., "childhood"—renders the child vulnerable to a variety of risks, it is vital to the optimization of human intelligence; by improving the child's nutritional status (and, obviously, its survival), the capability of the adult brain is equally improved. Therefore, a child's ability to optimize its intellectual potential would be enhanced by the consumption of foods with a higher protein and calorie content than its mother's milk; what better foods to nourish that weanling child than meat, organ tissues (particularly brain and liver), and bone marrow, an explanation first proposed by Bogin (1997).

Early weaning and the resultant weanling's dilemma appear to illuminate the primary importance of the large human brain and its cognitive abilities in human evolution. If selection had favored only the survival of the child, we would nurse long and wean late, as other hominoids do. Yet, we would not have our large brain. Instead, humans wean early, putting the child at risk, but supporting, through the consumption of adult foods, the prolonged and expensive fetal rates of brain growth and, therefore, intellectual potential. Early weaning is a strategy, then, that supports a pattern of brain growth that enhances intellectual capability (social, extractive, and technological skills); these, in turn, will serve to enhance the child's reproductive fitness and success if he/she survives to adulthood.

Early weaning in an evolutionary perspective

Assuming that the weaning behavior seen in the living great apes reflects the ancestral pattern, early weaning in anatomically modern *H. sapiens* represents a derived condition. At some point in our evolutionary history, then, hominins began to deviate from the ancestral pattern, weaning their youngsters at increasingly younger ages, until the modern timing, between 2-3 years, was reached. In modern humans, early weaning is associated with a unique pattern of brain growth, and both may have co-evolved through a feedback mechanism, as increases in brain size demanded still earlier weaning to provide nutritional support for both the brain's increased growth and size. However, given the severity of the weanling's dilemma, such co-evolution seems unlikely unless the earlier weaning was offset by a significant reproductive advantage. Such an advantage would probably occur only after increases in brain size had improved cognition and technology sufficiently to counteract at least some of the problems facing the weanling. Alternatively, however, evolutionary shifts sometimes first appear in the service of one need, and later shift, only then coming to serve their current function. Early weaning may be one such pre-adaptation or exaptation, first appearing in the service of a need quite different from its modern role of supporting the large brain and the prolonged period of rapid brain growth necessary to achieve it.

It is proposed here that a trend toward earlier weaning may have begun in the hominin line at the same time a tool-assisted dietary shift first appeared in the fossil record at ca. 2.5-2.6 Ma (de Heinzelin et al., 1999; Semaw et al., 2003). At that time, the use of stone tools may have significantly improved the quality (sensu Leonard and Robertson, 1994) of the hominin diet. Modern forest-living chimps use hammerstones to process certain large, nutritionally dense, but well protected nuts, such as *Panda* sp. and *Coula* sp. (Boesch and Boesch, 1983). These and a few other nut and seed-producing species may have long been a part of the hominoid diet (Schoeninger et al., 2001). However, at ca. 2.5-2.6 Ma, the hominin stone tool repertoire expanded well beyond the ancient use of natural hammerstones. At the Gona site, Ethiopia, retouched flakes, bifacial cores, and "knife-like flakes" made on well selected raw materials were found in close association with equid and bovid bones bearing cut marks (Semaw et al., 2003). Stone tools and associated fauna were also found at Hadar, dating to 2.3 Ma (Kimbel et al., 1996). At the site of Bouri, 90 km away, bones bearing cut marks and other modifications confirm butchery and carcass manipulation, while the absence of directly associated lithics suggests that stone tools had now become important enough for their curation and conservation in areas where appropriate raw materials were rare (de Heinzelin et al.,1999). Unequivocally, then, tool-assisted faunivory, presumably reflecting scavenging rather than hunting, had been established by ca. 2.6 Ma. On the other hand, stone tools without associated fauna have been identified at Lokalalei, Kenya (Roche and Delagnes, 1999), confirming their importance and suggesting, perhaps, that tools were now being used in a wider range of activities, including the processing of perishable materials.

The evidence of defleshed and butchered carcasses (de Heinzelin et al., 1999) represents an important shift in hominin behavior and shows not only that carcasses were being acquired soon after death, but that hominins were able to control those carcasses for some period of time, a pattern that has been termed both "power scavenging" (Bunn, 2001) and "confrontational scavenging" (Van Valkenburgh, 2001). If we accept that the behavior of living chimps reflects, in a general way, that of early hominins, then this evidence represents an entirely new behavior. First, while chimps use tools and eat meat, tool use by chimps in the context of meat eating appears to be very limited and is restricted to marrow picks and leaf sponges (e.g., Whiten et al., 1999), as prey are dismembered manually. Second, chimps generally acquire their meat through active hunting, not scavenging (see review in Stanford, 2001). They very rarely consume carcasses (Toshikazu et al., 1983; Hasegawa et al., 1983; Muller et al., 1995); they appear to dislike the taste or they fail to recognize the carcass as food. If the latter is true, then by ca. 2.6 Ma, an important shift had occurred in the earlier hominin "prey image" (e.g., Boesch and Boesch, 1989). In the Carnivora, the prey image is very conservative, changing only slowly and under persistent and unusual environmental conditions (Baron, 2004). Thus, the shift to tool-assisted butchery and the consumption of carcasses were significant and arguably constituted qualitative departures from the behaviors assumed for earlier hominins. In any case, such activities effectively made some hominins (presumably, but not necessarily, early *Homo*) part of the African carnivore guild (Van Valkenburgh, 2001). Such an alliance brought with it both costs and rewards and each may have played a role in the development of early weaning in different ways.

For example, the acquisition of carcasses may have been accompanied by new and significant risks and altered patterns of mortality. Plio-Pleistocene African Carnivora were more numerous both in terms of species (nine as opposed to five today) and in terms of population density (Van Valkenburgh, 2001). Therefore, even though herbivore biomass may also have been large, intraguild competition for prey and carcasses may have been considerable (Van Valkenburgh, 2001). Moreover, as hominins moved into the carnivore guild, they were no longer simply prey, but by that action had also become competitors, "adding," as Van Valkenburgh (2001: 101) has dryly noted, "a new incentive to kill them." It seems possible, then, that their new dual role in the carnivore guild as both competitor and prey may have taken a heavy toll on the most active, meat-seeking members of the hominin group, i.e., the young adults.

While it is not clear that paleodemographic data can accurately represent ancient mortality patterns (e.g., Koenigsberg and Frankenberg, 2002), the limited information available for Pleistocene *Homo* and for prehistoric anatomically modern foragers suggests that the move into the carnivore niche may have been a dangerous one. Whether meat was acquired as a carcass or hunted live, it was a dangerous activity. In one sample of European *H. heidelbergensis*, for example, "only two individuals lived beyond" their third decade (n = 32) (Bermudez de Castro and Nicolas, 1997: 339). In his survey of Neandertal mortality, Trinkaus found that more than 50% of the known sample was dead before the age of 40 (1995:131). While the mortality data for early *Homo* are suspect because of small and fragmented samples, a very similar pattern of high levels of young adult mortality was also found in several larger and later samples of prehistoric anatomically modern foragers: at Libben and Jomon, pre-40 mortality was 69.5% and 79% respectively (Trinkaus, 1995). This issue has been explored in greater depth elsewhere (Kennedy, 2003; Kurland and Sparks, 2003; Figs 3 and 4). Causes of death are generally difficult to determine in skeletal samples, but high levels of trauma were noted in the Neandertal sample (Berger and Trinkaus, 1995) and in a number of forager samples (Angel, 1974; Larsen, 1995:116-118). In fact, in the Neandertals, virtually every individual who lived to adulthood demonstrated "at least one (minor or major) defect" (Berger and Trinkaus, 1995: 841). These authors concluded that such high levels of trauma may have been associated with a hunting pattern involving active confrontation (Berger and Trinkaus, 1995).

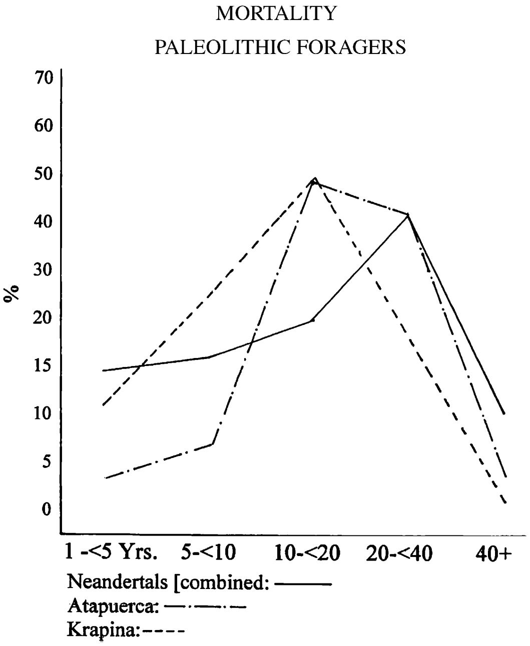

Fig. 3. Mortality for Paleolithic foragers. Neandertal data ("combined" and Krapina) from Berger and Trinkaus, 1995; Atapuerca: Bermudez de Castro and Nicolas, 1997. Modern humans show a U-shaped "Class 1" mortality curve, with maximum mortality early and late in life. Elevated rates of young adult mortality in the Paleolithic groups form "Class 2" mortality profiles; this pattern of mortality would require a shift in strategies for raising slowly developing human youngsters; those strategies may have included alloparenting and adoption, already well established in non-human primates, and a new strategy involving earlier weaning.

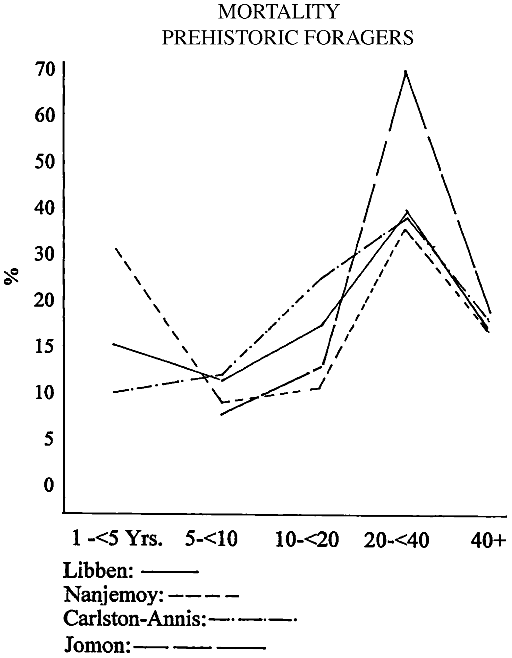

Fig. 4. Mortality of prehistoric foragers. While the Paleolithic data represented in Fig. 3 are very imperfect, larger samples of anatomically modern, prehistoric foragers also show a very similar Class 2 profile with elevated mortality in young adults and, consequently, low rates of survival into the older age grades. Data for Libben: Lovejoy et al., 1977; Nanjemoy: Ubelaker, 1974; Carlston-Annis: Mensforth, 1990; Jomon: Kobayashi, 1967.

Larsen (1995: 117), in an extensive review of the data, found that forager populations generally have higher levels of "accidental" trauma than do agriculturalists.

Young adults are also likely to be parents of young children and, assuming that the available mortality profiles reflect, in a general way, an actual pattern of heavy young adult mortality in these populations, what strategies might have been used to enhance the survival of youngsters whose parents had died before their independence? Although hunting is generally a male-dominated activity, there seems to be few reasons that the acquisition and manipulation of carcasses should also have been limited to males. Claims that the high young adult mortality at Libben, for example, could not reflect a stable population (Howell, 1982; Milner et al., 1989) overlook the existence, in both human and non-human primate societies, of strategies that could improve the survival of orphaned youngsters. Such strategies include alloparenting and adoption.

Allison Jolly (1985) made the important observation that among primates, parenting consists of several separate and non-overlapping components, such as feeding, protection, socialization, carrying, and nurturance, each of which may be provided separately and by individuals other than the birth parents. Obviously, such compartmentalized and "redundant" (Jolly, 1985) care could be effective when a parent is ill, absent, or dead. In modern humans, in fact, child care by individuals other than the birth parents is so widespread that it has been termed "the hominid adaptation" (Lancaster and Lancaster, 1983). Others have noted that "nonparental caretaking is either the *norm* or a *significant form* of caretaking in *most* societies" (Weisner and Gallimore, 1977; emphasis added). Such alloparenting is usually explained either within the context of kin-selection (e.g., Blaffer-Hrdy, 1976) or as a way for subadults to observe and learn adult skills prior to parenthood (e.g., Lancaster, 1971), or as some combination of these factors; its origin, however, may be explained equally or in part by the need to provide care for still-dependent youngsters when one or both parents have died. Despite the predictions of life history theorists that slowly maturing species should also have long lives (Sterns, 1992; Charnov, 1993), non-parental, alternative caregivers are frequently found in slowly maturing, K-selected species (Spencer-Booth, 1978; Reidman, 1982). While this practice may, indeed, serve to introduce subadults to adult behaviors, particularly among related individuals, it may also serve as a survival strategy in the case of premature parental death.

While the death of a mother before her youngest child's nutritional independence is, for non-human primates, often fatal for the infant as well, adoption of nursing non-human primate infants has been reported, albeit rarely, in *Gorilla* (Fossey, 1979), *Pongo* (Becker, 1972), and *Pan troglodytes* (Palthe and Hooff, 1975). In addition, such behavior appears frequently in cercopithecoid species (see reviews in Quiatt, 1979; Thierry and Anderson, 1986). While alloparenting and adoption would enhance the survival of orphaned, but still-nursing young, early weaning, too, could serve to enhance the survival of such youngsters. The survival of these youngsters would depend, in part, on their age and on the availability of appropriate (soft, easily digestible, and relatively pathogen-free) weaning foods. Among modern foragers, weaning foods generally consist of pre-masticated starchy plants or meats (Sellen and Smay, 2000). Although some researchers have claimed that plant foods (e.g., roots and tubers) may have played an important role in human evolution (e.g., O'Connell et al., 1999; Wrangham et al., 1999; Conklin-Brittain et al., 2002), the low protein content of "starchy" plants, generally calculated as 2% of dry weight (see Kaplan et al., 2000: table 2), low calorie and fat content, yet high content of (largely) indigestible fiber (Schoeninger et al., 2001: 182) would render them far less than ideal weaning foods. Some plant species, moreover, would require cooking to improve their digestibility and, despite claims to the contrary (Wrangham et al., 1999), evidence of controlled fire has not yet been found at Plio-Pleistocene sites. Other plant foods, such as the nut of the baobab (*Adansonia digitata*), are high in protein, calories, and lipids and may have been exploited by hominoids in more open habitats (Schoeninger et al., 2001). However, such foods would be too seasonal or too rare on any particular landscape to have contributed significantly and consistently to the diet of early hominins. Moreover, while young baobab seeds are relatively soft and may be chewed, the hard, mature seeds require more processing. The Hadza pound these into flour (Schoeninger et al., 2001), which requires the use of both grinding stones and receptacles, equipment that may not have been known to early hominins. Meat, on the other hand, is relatively abundant and requires processing that was demonstrably within the technological capabilities of Plio-Pleistocene hominins. Meat, particularly organ tissues, as Bogin (1988, 1997) pointed out, would provide the ideal weaning food.

The carcass itself may have played both nutritional and non-nutritional roles in human evolution. Although chimps are highly social, feeding is generally an individual effort. Therefore, most extractive tool use (nut smashing, termite fishing) occurs during solitary or semi-solitary (mother/infant) activities. Meat, because it is shared by a group, provides an immediate context for the social transmission of a new behavior, and because it is super-abundant, competition would be reduced and social tolerance would consequently be elevated (Fragaszy and Visalberghi, 1990; van Schaik et al., 1999). Thus, the carcass and the behaviors it engenders could have played an important role in the development and transmission of new behaviors, such as tool manufacture and use. Moreover, the nutritional value of even part of a single carcass of, for example, a 50 kg antelope is substantial (see table 2 in Kaplan et al., 2000; Speth and Spielmann, 1983).

Meat: who benefits?

Three age categories of hominins, in particular, would have benefited nutritionally from this new strategy; these benefits may have appeared at different points along an evolutionary timeline. In an ontogenetic sense, the earliest benefit from a high quality diet (sensu Leonard and Robertson, 1994) may have been not to an adult, but to a fetus. In modern women, the adequacy of a woman's nutrition during pregnancy directly affects the birth weight of the infant she carries: women whose own nutrition is impaired generally give birth to low-birth-weight babies (Abrams, 1991). One review of neonate mortality noted: "The birth weight of an infant is the single most important determinant of its chance of survival and health, growth and development" (Edelman, 1990: 233). Data from other species suggests that the relationship between maternal nutritional status and neonatal birth weight may be a generalized phenomenon across the Mammalia (e.g., Bloomfield et al., 2003). Currently in the United States, 66% of all human neonatal deaths are directly related to low birth weight (Abrams, 1991), a factor that is directly proportional to their weight (McCormick, 1985), and is most often due to retarded intra-uterine growth, rather than to prematurity (Jelliffe and Jelliffe, 1978). Moreover, if a mother is not herself fully grown, her own nutritional needs, related to her ongoing growth, must be added to those of the fetus (Frisancho et al., 1985), elevating her nutritional needs during pregnancy.

Abundant cross-cultural data clearly indicate that dietary improvement during pregnancy will increase neonatal birth weight and may substantially reduce perinatal and infant mortality (e.g., Peru: Frisancho et al., 1977; Gambia: Prentice et al., 1987). Single nutrients are less important, however, to fetal growth than to overall maternal nutrition, and dietary protein is indirectly, rather than directly, related to fetal growth. For example, if maternal caloric needs are not met during pregnancy, then dietary protein will be used for her energetic needs rather than for fetal tissue synthesis (Abrams, 1991). Thus, the addition of higher quality food items such as meat to a pregnant woman's diet could significantly affect the survival of her offspring. Inadequate maternal nutrition may result, therefore, not only in poor infant growth but in maternal depletion, reflected in an extended IBI and reduced completed fertility. The captive primate studies cited above indicate that optimum maternal nutrition may optimize infant growth, thereby providing a foundation for early weaning. Therefore, reproductive age females, as well as their fetuses and infants, would clearly benefit from improved amounts of protein and calories. Adult males and post-reproductive females would also benefit, but comparatively less. Such foods, if regularly available, would enhance a child's chance, first for survival, and second for optimum intellectual development. Bogin and Smith (1996; Bogin, 1999a,b), using slightly different logic and evidence, made a similar suggestion, emphasizing the benefit of early weaning to the mother.

As suggested above, the benefits to the weanling child would, perhaps, have been the most important in terms of human evolution in serving not only the child's developmental needs, but through that child, the group to which it belonged. Anthropologists have long noted the importance of the "5 to 7 shift" (e.g., Weisner, 1996) when the child leaves the pre-operational stage of infancy and enters the more focused and controlled concrete operational stage. In modern societies, this is a time when social skills first become reciprocal, when the child assumes new functions within the group, and begins to understand social and political alliances. The child also begins to contribute to group welfare, acting as sentinel and gathering food for others (see discussion in Weisner, 1996); it is, in short, as Weisner noted, an apprenticeship for adulthood.

In these scenarios, then, meat would have been both a cause and an effect of early weaning: causative, as the dangers associated with the acquisition of carcasses may have resulted in elevated death rates for young parents, forcefully necessitating early weaning, and an effect, as the carcass provides not only uniquely nutritious and easily digestible tissues but a vehicle for the social transmission of new ideas and skills. Thus established, early weaning would later provide both the foundation and the support for our unique pattern of brain growth.

Conclusions

According to life history theory, slowly developing organisms should also have long life spans in order to ensure survival, particularly of the later-born young. While modern human populations do, indeed, have long life spans, historical data indicate that this has not always been true, and that significant old age survivorship (>50 years) began only after the Industrial Revolution (Acscadi and Nemeskeri, 1970). Among the slowly developing precocial mammals, such as the Primates, mortality is normally density-dependent (related to competition for limiting resources), while in more rapidly developing altricial mammals, like the Carnivora, mortality is instead generally independent of density (related to stochastic events) (MacArthur and Wilson, 1967; Pianka, 1970). When the precocial hominins moved into the carnivore niche, they encountered new hazards that their evolutionary heritage had left them unequipped to handle. Among those young adults who were now functioning as carnivores, yet lacked their claws, piercing and shearing dentition, and speed, mortality may have been high. In this explanation of the origin of early weaning, the acquisition of meat serves as both a cause and a solution: acquiring meat exacted a heavy toll on young parents while also providing highly effective nourishment for weanling orphans. While mortality data are poor for earlier human species, archaeological data for prehistoric modern human foragers suggest that elevated rates of young adult mortality may have been common, reflecting the risks associated with the acquisition of meat, either through scavenging or hunting. The fact that slowly developing K-selected primate young are not always raised by their birth parents may be reflected in the widely found strategies of alloparenting and adoption.

Increase in the size of the human brain is based on the retention of fetal rates of brain growth (Martin, 1983), a unique and energetically expensive pattern of growth characteristic of altricial mammals (Portmann, 1941; Martin, 1984). This research now adds a second altricial trait—early weaning—to human development. The metabolically expensive brain produced by such growth rates cannot be sustained long on maternal lactation alone, necessitating an early shift to adult foods that are higher in protein and calories than human milk.

If selection had targeted only the survival of the child, then humans would have continued to nurse long and wean late, like the other hominoids. Yet doing so would have prevented not only the development of our large brain, but would also have prevented increasing population numbers and the vital genetic diversity that accompanies population growth. It has been argued here that selection favored early weaning because the early shift to adult foods, despite the hazards to the weanling, supports the child during a critical period of neurological development; thus, selection in humans has favored not merely the survival of the child, but the intellectual potential of that child. The evolutionary tradeoff is harsh, but it was the only way we could have attained our large brain. This argument supports Barry Bogin's (1997) suggestion that in early societies, the weanling could best be supported on a diet including marrow, brain, and other animal tissues acquired initially through scavenging and later by hunting. It seems logical that the beginnings of this pattern appeared with the origin of more active meat-seeking behaviors, by ca. 2.5-2.6 myr ago. This shift provided the nutritional support for the initial expansion of the brain, and the origin of the genus *Homo*, which the fossil record suggests occurred soon after that time.

If we assume that the behavior of modern chimps reflects, in a general way, the behavior of pre-*Homo* hominins, then ca. 2.5-2.6 Ma, two important behavioral shifts away from that primitive pattern occurred, one dietary and one technological. These behavioral shifts acquire a new significance when viewed within the context of an emergent pattern of early weaning. First, at Gona, there is evidence that hominins were using well made stone tools to process meat (Semaw et al., 2003), and second, meat apparently had not been hunted live, but was scavenged as carcasses. These two critically important behavioral shifts significantly increased not only the quantity of food available on a particular landscape, but its quality as well, significantly changing patterns of hominin survivorship. Such a dietary shift would have particularly benefited three groups: the developing fetus, lactating females, and weanling children. Although the advantages to the fetus and to mothers may have appeared earliest, it was the weanling child who benefited most, in an evolutionary sense, since it is during childhood (before 7 years of age) that the structure and capability of the adult brain is established.

Although the taxonomic identity of those first scavengers remains unknown, it may have been an innovative and "smart" australopith (*A. garhi*? Asfaw et al., 1999). Evidence from a number of non-human primate species suggests that innovative activities are often initiated by a single, clever individual (Itani, 1965; Kummer and Goodall, 1985), often a youngster who developed a new behavior during play, which then spread throughout the group (Itani, 1965; Fragaszy and Visalberghi, 1990). It is not difficult to imagine a scenario in which play involving a nut-processing hammerstone was shifted to a nearby carcass, leading to the discovery of a new and effective way to acquire brain and marrow. This shift in the earlier hominin's "prey image" led to the recognition of the carcass as food, effectively changing the course of later human evolution.

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