Chapter 18

EVOLUTION OF HUMAN LACTATION AND COMPLEMENTARY FEEDING: IMPLICATIONS FOR UNDERSTANDING CONTEMPORARY CROSS-CULTURAL VARIATION

D.W. SELLEN

Departments of Anthropology, Nutritional Sciences and Public Health Sciences, and Centre for International Health, University of Toronto, 19 Russell St., Toronto, Ontario, M5S 2S2, CANADA. dan.sellen@utoronto.ca

1.   INTRODUCTION

   Artistic reconstructions of ancestral hominids [1] often depict mothers with bared breasts and suckling infants, reflecting assumptions about the importance of lactation in human evolution. However, anthropologists have published no detailed theories about how our ancestors fed young children. In the absence of a scientific model of the evolution of human lactation and complementary feeding, it is difficult to evaluate claims made about the long duration of ancient breast-feeding or the "naturalness" of lactation patterns observed in some human societies. This chapter therefore has two main goals. First, I review several lines of evidence that suggest how changes in birth spacing, foraging strategy and sociality may have increased the selective advantages of a more flexible pattern of lactation and a behavioural shift towards complementary feeding in past environments. Second, I develop a hypothesis that the complementary feeding of young children is a fundamental component of life and socio-behavioural adaptations that evolved among our human ancestors as an ecological strategy for increasing maternal fitness. I suggest that the ancestral habit of introducing

safe complementary feeding after a period of exclusive breast-feeding is unique to humans. It is linked to the evolution of a species-typical care giving "package", which includes social foraging, food sharing, food processing, and a capacity to invent technological solutions to dietary challenges. I conclude with a brief review of how changes in social organisation, time allocation and diet quality that accompanied the agricultural and industrial revolutions have created an environment in which the evolved tendency to introduce foods to breast-feeding young undermines the health of populations.

1.1 Background

As with most human behaviours, young child feeding practices occur in bewildering variety across cultures [1-5] and change over time.[6-11] Lactation researchers and policy makers have struggled to document this variation by developing indicators for the biologically salient aspects of breast-feeding [12-13] and complementary feeding.[14] Such efforts have been driven by the discovery that some young child feeding practices are causally associated with poor growth, delayed development and increased morbidity and mortality. These include never breast-feeding, partial breast-feeding in the first half of infancy, cessation of breast-feeding before the third year of life [15-16] use of contaminated and often nutritionally inadequate complementary foods [17-19] and passive feeding. [20] Over the last quarter of a century expert groups have proposed a series of recommendations for young child feeding based on observation of clinical outcomes. These have been adopted by global, national and non-governmental health organisations.[21-23].

Clinical concern about the *consequences* of variation in infant and young child feeding practices has meant that fewer studies have attempted to identify their root *causes* in social and environmental conditions or to develop broad interventions to address them. [24-26] Health providers tend to assume that many deviations from clinical recommendations are attributable to unmeasured "cultural" factors, and that these are randomly distributed across societies (i.e. arbitrary), and fixed within societies (i.e. difficult to modify).

Such assumptions are not well tested, and divert attention from important questions about why human breast-feeding patterns are so labile, and why so apparently arbitrary? In developing a conceptual framework in which to understand contemporary variation, it is useful to consider the evolutionary history of human lactation and complementary feeding. Reconstruction of this evolutionary history from comparative biological evidence has the potential to reveal co-evolved links between human diet, life history and behaviour that continue to influence the way people feed infants today.

2.   **EVOLUTION OF HUMAN LACTATION**

2.1   **Origin**

It may never be possible to ascertain when lactation evolved or what initial selective advantage it conferred because soft tissues are rarely preserved as fossils.[27-28] There is little doubt, however, that lactation was an ancient innovation. Mammary glands of extant monotremes, metatherians and eutherians are sufficiently similar in detail to suggest a monophyletic origin.[29] Analyses of several hundred nuclear gene sequences [30] of the amino acid sequence of [alpha]-lactalbumin protein [31] and of the BRCA1 and IGF2 receptors [32] suggest that divergence of therian mammals and monotremes, and of marsupials and placentals, took place somewhere between 163 and 238 million years ago (MYA), and between 161 and 192 MYA respectively.

These molecular divergence–time estimates are reasonably well supported by a fossil record. A diverse group of mammaliaform insectivores such as *Morganucodon* and *Hadrocodium* appear by at least the early Jurassic (200 MYA).[33-34] Probably descended from egg-laying therapsid reptiles, their cranial-dental morphology suggests they had a fully functioning temporomandibular joint (which in extant mammals develops after the suckling stage in extant monotremes and therians), dyphyodonty (reliance on a single set of specialised permanent teeth that grew after a single set of presumptive "milk" teeth), and several other mammalian synapomorphies (shared, derived traits indicating common ancestry). Dental evidence of highly specialised nipple latching among marsupial alphodontids of the late Cretaceous [35] supports a hypothesis that variation in lactation biology observed among extant mammals is also very ancient.

Lactation almost certainly originated as an increased secretion of carotenoids, antibodies, white cells and other immunity-boosting factors onto eggs or in glandular secretions licked by young.[36-37] Mammary glands are structurally and ontologically similar to tetrapod epitricheal (sebaceous and apocrine) glands, which have the capacity to synthesise carbohydrates, proteins and lipids.[38] It is therefore likely that the addition of nutritive factors to these early secretions triggered selection for an improved capacity of early mammals to quickly store and release energy and nutrients.[39-40] Lactation provided ancient mammals with a new mechanism for scheduling growth and reproduction across the lifespan.[41] The functions of lactation are nowadays three and so important that they are shared by all extant species.[42] They are: (i) immune protection and reduced exposure to dietary pathogens; (ii) a supply of energy and nutrients fine-tuned to juvenile needs and buffered by maternal body stores; and (iii) fertility regulation calibrated to

maximise maternal fitness through promoting optimal litter spacing for infant survival.

2.2   Co-evolution of lactation, life history and feeding ecology

Whatever the precise selective mechanism, the origin of lactation had large implications for the subsequent evolution for mammalian life history and behaviour. Lactation altered the developmental, behavioural and social links between mothers, offspring, and indeed fathers. It opened a developmental window of opportunity for learning through juvenile play and social interaction and made possible the evolution of gestation among therians. Thus, it underpinned the adaptive radiation of mammals.

Many features of lactogenesis [43-44] and immunological activity [37] are remarkably conserved across species. Species differences in other aspects of lactation biology, such as milk energy content, yield, nutrient composition and immune factors probably indicate adaptive modifications that increase fitness in a range of ecological niches with different disease exposure and nutritional challenges.

Within mammal clades, lactation co-evolved with changes in life history strategy and feeding ecology. Lactation length is strongly correlated with adult female mass.[45] It is relatively longer (for body size) among marsupials, bats and primates, and relatively shorter among earless seals and baleen whales. Milk volume, gross composition and peak yield are clearly linked to the behavioural ecology of infant care.[46-47] For example, terrestrial species that nurse continuously (e.g. marsupials) or on demand (e.g. primates) produce dilute milks that are high in carbohydrate and low in fat; terrestrial species that nurse episodically (e.g. felids and canids) produce milks high in fat and carbohydrates, and protein; marine mammals (e.g. phocids) produce relatively concentrated, fatty milks. Species with smaller bodies or relatively faster life histories tend to secrete more nutrient dense and fatty milk at higher rates.[29, 48-49]

Figure 18-1 summarises the behavioural ecological aspects of the post-natal development of feeding in most modern mammals. Juvenile daily intake of energy and specific nutrients increases after birth due to increased milk intake during an initial period of exclusive suckling. Ingestion of foraged foods marks the beginning of a "transitional feeding" period during which milk continues to contribute to nutrition and immune protection but juveniles can increase total intakes beyond peak maternal milk production. As juveniles begin to derive nutrients more efficiently from the environment than from the mother (due to some combination of increased competency, decreased milk production and increased maternal resistance to suckling),

both the absolute and the proportional contribution of milk intake decreases until last suckling occurs. After weaning, independent foraging achieves further increase in total intake. In a minority of species, juveniles may consume provisioned foods foraged by mothers or allo-caregivers both before and after weaning. Milk consumption provides immune benefits during the exclusive and transitional feeding periods. These are tailored at all ages to juvenile development and pathogenic exposure, and persist beyond weaning.
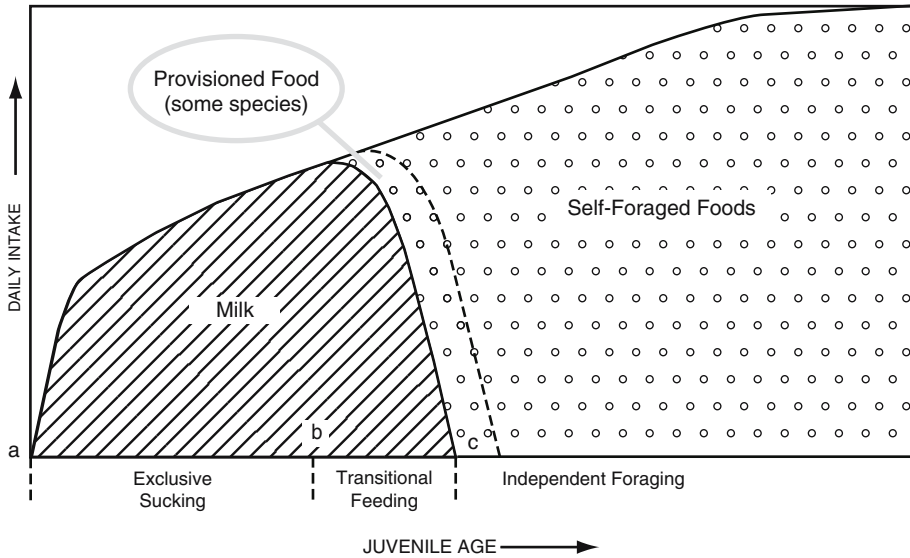

Figure 18-1. Postnatal development of feeding in a typical mammal. Key: (a) birth; (b) ingestion of foraged foods; (c) last suckling (i.e. weaning).

The age at first solid food relative to the age at weaning has been interpreted as an indicator of the function of lactation within the life history and feeding ecology of a given mammal.[45] A longer period of transitional feeding, i.e. first solid food eaten well before weaning, is common among mammals with single, precocial offspring. In these mammals the energetic and nutritional constraints on lactation may be less important in shaping the evolution of life history than the benefits of maintaining contact between mother and young, such as increased opportunities for learning social or foraging behaviour. A shorter period of transitional feeding, i.e. first solid food eaten near weaning is common in polyctocous species with altricial young. In these species the young are very dependent on milk and maternal constraints on lactation may be critical.

A relatively longer duration of exclusive suckling may be interpreted as an evolutionary response to the relative difficulty of acquiring, ingesting or digesting the adult food. An alternative hypothesis is that a relatively abrupt transition from exclusive suckling to weaning can only evolve when the adult diet is more nutrient dense. In some species with "difficult" adult foods juveniles take partially chewed food (e.g. hystricomorph rodents), regurgitated food (e.g. wolves) or modified fecal matter (e.g. koala bears) from the mother and occasionally other adults.

2.3   Transitional feeding in non-human primates

Detailed studies of the diets and foraging behaviour of non-human primate weanlings are few but variation in transitional feeding patterns is apparently wide both within and between species and has yet to be fully described and explained.[50-51] In general, non-human primate infants wean relatively abruptly and begin to forage on foods similar to those selected by the mother, processing them largely for themselves. They therefore fit the general mammalian pattern depicted in Figure 18-1.

Comparative zoological analyses have generated several models to predict duration of lactation (i.e. age at weaning) from other primate life history traits. These include: 1.5 times the length of gestation [52], eruption of first molar teeth [53-54], quadrupling of birthweight [55], and attainment of one-third adult weight. [56] However, no model reliably predicts age at weaning for all species, suggesting that it is quite labile relative to other life history traits.

Weaning age appears to be sensitive to ecological factors that constrain maternal ability to meet the increasing energy needs of growing offspring [55] and the ability of infants to survive without mother's milk. Colleagues and I recently conducted a preliminary test of a hypothesis about variation in the patterning of non-human juvenile primate feeding ecology.[57] We predicted that ecological constraints result in shortened duration of transitional feeding in species where adults exploit a relatively high quality diet. Among 23 species of non-human primate for which data are available, the duration of transitional feeding (estimated as the period between reported age at first consumption of solid food and age at last suckling) is found to increase with maternal body size (Figure 18-2).
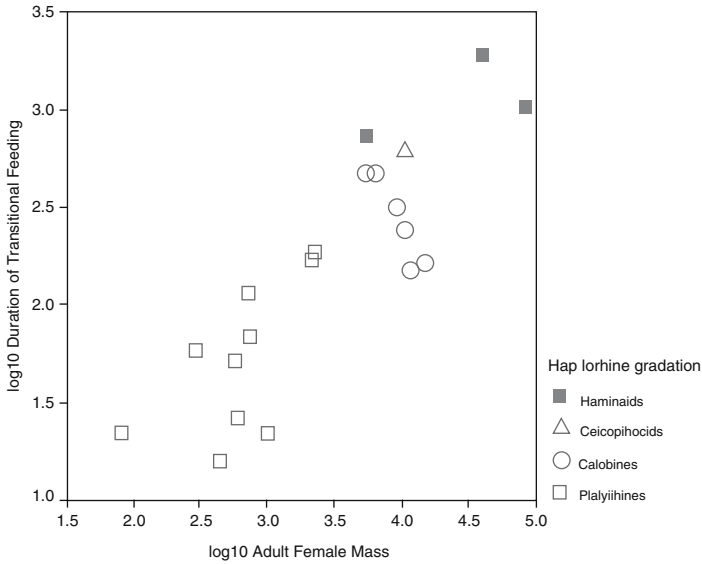
Figure 18-2. Relationship between duration of transitional feeding and body size in a sample of non-human primates (n=23).
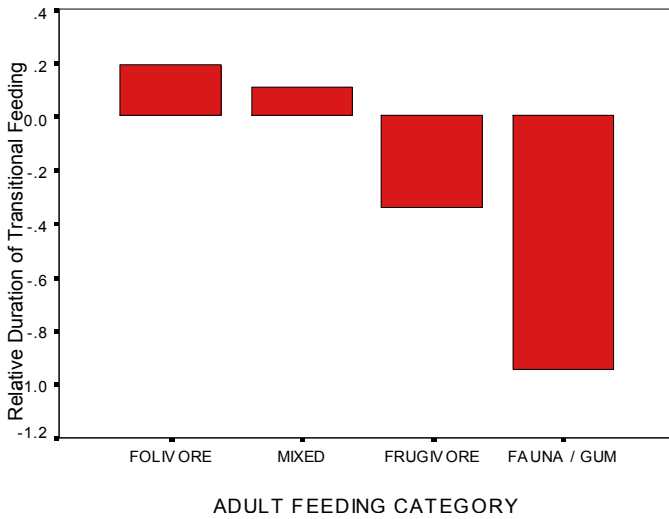

Figure 18-3. Relationship between adult feeding category and relative duration of transitional feeding (calculated as residuals of the log-log plot against body size) in a sample of non-human primates (n=23). $F_{3, 23} = 2.611$, $p = 0.087$.

We controlled for large species differences in body size by comparing residuals of the least-squares regression with maternal body size (Figure 18–3). This suggested that transitional feeding was of relatively short duration among gummivores and faunivores, and relatively long among folivores and mixed feeders. These results do not control for phylogeny or group size and other aspects of ecology, but do suggest that diet quality constrains primate weaning. Non-human primate species wean relatively quickly when they have access to better quality foods.

3.   SHARED AND DERIVED FEATURES OF HUMAN LACTATION

3.1   Breast milk composition, secretion and delivery

Lactation researchers continue to discover important ways in which human milk differs from that of domesticates such as cows, goats and sheep. Nevertheless, there is nothing particularly unusual about the gross characteristics of human milk in comparison to species with which we share more recent common ancestry. Lactation has been poorly studied among our closest living relatives, the apes, but it is known that gross composition of human milk falls within the range of non-human primates.[58-60] Although human milk contains one of the lowest concentrations of protein and highest concentrations of carbohydrate of any mammal, it is not a remarkable outlier among primates. There is little evidence to suggest that relatively rapid post-natal human brain growth is associated with significantly modified milk.[61] Human milk production is similar to that of other anthropoids when measured on a volume yield and energy output basis scaled for body size. [62] Humans share a general primate pattern of low milk yield, assumed to have co-evolved with low reproductive rates and slow life histories relative to body size.[46,49,63] Unlike other mammals, which may for ecological reasons feed infrequently and have fatty milk, extant primates keep their infants with them at all times, allow frequent suckling and are therefore adapted to produce relatively modest volumes of energy dilute milk that contains relatively high lactose and low protein and fat fractions.[64]

Among primates there is some variation in the number, position and gross morphology of mammary glands.[65] Some theorists have drawn attention to the unique shape, pubertal development and unusual life-long visibility of the human breast, and hypothesised that a derived, secondary function in signalling reproductive potential has evolved.[66-67] However, these

unusual characteristics can be explained more simply. First, the morphology of the human breast probably reflects an evolved structural modification to accommodate suckling by a snoutless baby (Gillian Bentley, personal communication). Second, the pubertal development of this structure involves complex and presumably costly metabolic processes.[68] Scheduling of investment in these processes before ovarian maturation probably resulted in a selective advantage because it was more efficient than repeated resorption and elaboration of breast tissue between successive pregnancies.

3.2   Maternal metabolic accommodation

Several lines of evidence indicate that lactation places significant metabolic demands on non-human primate mothers and that mechanisms exist to accommodate these demands.[69-73] Captive studies in some species suggest that the energetic costs of lactation are met by a suite of energy-sparing adaptations that include breakdown of tissue stores [74], increases in the efficiency of energy utilisation [75], reductions in physical activity [74, 76], and shared care of infants.[77] Field observations show that intake of high-energy foods [78], overall food energy [79-80] and time allocated to foraging [81-82] increase among lactating females, particularly when forage quality is poor.[83] Evidence that wild non-human primate mothers successfully accommodate the costs of protecting their infants against fluctuations in milk supply and quality when conditions are adverse is scant.[71]

Humans may have evolved additional types of adaptation to reduce the maternal cost of lactation relative to that of other primates. These adaptations include appreciable fat storage during pregnancy, relatively slow infant growth, flexible scheduling of weaning and complementary feeding.

3.3   Maternal fat storage

In humans a number of physiological mechanisms reduce the daily costs of lactation when conditions are favourable. The average woman begins lactation with approximately 125 MJ of additional fat accumulated during pregnancy.[84] Depletion of these reserves has the potential to subsidise the energy costs of lactation by ~118.6 MJ (0.325 MJ/d) in the first year of infant life, equivalent to a significant proportion of the total energy required for milk production when fully breast-feeding into the second year. This storage of fat demands the largest proportion (~71%) of additional energy needed to sustain a healthy pregnancy in non-chronically energy deficient women. [84-86] But it is achieved with only modest alterations in maternal energy flux and metabolic partitioning.[87] Many individuals accommodate a proportion

of the daily energy cost of pregnancy by reductions in basal metabolic rate and physical activity. In such individuals, the average daily costs of pregnancy (~0.7 MJ/d) are low (~8%) in relation to the usual dietary energy intakes and requirements of healthy non-pregnant, non-lactating women (~8.78 MJ/d).

3.4   Slow infant growth

In almost all mammals the immediate post-natal linear growth proceeds at a similar rate as *in utero*. Weight gain is more rapid, at least during the suckling period.[39] Indeed, the weight of the fetus appears to be minimised for a given developmental stage. Although many species reach an advanced state of development *in utero*, deposition of offspring body fat reserves occurs almost exclusively after birth. In comparison to great apes, human neonates are relatively large [88] and fat. [89] Human infants grow more slowly [90], and juveniles grow for longer.[91]

Human infants appear to have low energy requirements in comparison to other primates, probably due to this slower growth. It has been estimated that, depending on age and sex, the average unit body mass requirements of human infants range between 0.34 and 0.38 MJ/kg/d (figures recalculated from references [92-93]) and include estimates for maintenance and activity. Even after controlling for Kleiber's allometric relationship between body size (W) and energy requirement (E ∞W 0.75), such estimates fall below those for free-living yearling baboons and captive large bodied cercopithecines, and within the range of daily intakes observed in much smaller sized (average 2.27 kg) wild yearling baboons.[94] Observation of *ad libitum* intakes among several species of captive large bodied cercopithecine infants results in estimates of average infant energy requirements in the range 0.837-1.255 MJ/kg/d.[95-96] Altmann's pioneering study of free-living yearling baboons (Papio cynocephalus) estimated their minimum total energy requirements for growth and maintenance at 0.871 MJ/d, or 0.383 MJ/kg/d (data recalculated from various tables in reference 97). At this age eight baboons in the sample were consuming a total 2.251 MJ of energy, of which approximately 40 % (i.e. 0.900 MJ/d) was estimated to come from milk.

3.5   Early and flexible weaning

There is no doubt lactation has remained a key life history component throughout hominid evolution. Current expert opinion based on clinical and epidemiological evidence is that infants have not evolved to make efficient use of other foods before six months.[16] Continued breast-feeding clearly remained a strongly selected component of ancestral maternal strategies, as

evidenced by its powerful anti-infective properties.[98] Today, humans benefit enormously from early exclusive breast-feeding and from partial breast-feeding continued into the third year of life, after which the marginal returns on continued breast-feeding diminish.

Nevertheless, weaning appears to have evolved to occur earlier in humans than evolutionary biologists would predict from our recent primate ancestry and current body size. A comparison of human and great ape life history parameters based on demographic data from hunter-gatherer populations shows that humans are distinctive in having a relatively low adult mortality, late age at first birth, long juvenile (i.e. pre-reproductive) period, long life span and high natural fertility (Table 18-1).

Comparative survival analysis of birth intervals in four hominoid species suggests that humans have the shortest ones. Although birth intervals rarely exceed 4 years in natural fertility human populations, half of all randomly-selected closed birth intervals exceed 4, 5 and 8 years in wild gorillas, chimpanzees and orangutans, respectively.[99] Since fertility ends at similar ages in human and chimpanzee females, human birth intervals are shorter and the "species-typical" rate of offspring production is higher.[100] As a corollary, even among hunter-gatherers human infants are weaned after relatively smaller post-natal weight gain.[101]

Nevertheless, as a species we are particularly good at keeping young alive, despite a well-established inverse relationship between birth interval and child survival in humans that is mediated by breast-feeding.[102-104] Infant and weanling survival is much greater among foragers than among apes, and greater still in non-industrial herding and farming economies.[105-108] Thus, ancestral humans evolved an unusual capacity to reduce the length of exclusive and transitional feeding without increasing mortality.

The scheduling of weaning is also unusually plastic among humans.[62] If suckling is initiated, duration of human lactation ranges from a few hours to more than 5 years, spanning the entire range observed for all other mammals.[109] In contrast to non-human primates, humans wean over a wide range of infant sizes. Anthropologists have sought to explain such flexibility as reflecting an evolved maternal capacity to vary reproduction in relation to ecology [110-112], the availability of alternate caregivers [113], and the specific flux of environmental and social factors influencing tradeoffs among the biocultural costs and benefits of weaning to mothers and infants.[114] Observation in contemporary human societies shows lactation behaviour is sensitive to maternal workload and the availability of cooperative childcare and feeding.[115-116] In sum, not only is the human lactation span comparatively short, but human mothers are clearly adapted to exercise more choice in the patterns and duration of breast-feeding than do other primates.

Table 18-1. Average values for hominid life history parameters

	Adult lifespan (1/M)	Age at maturity (1st birth, yrs)	Age at weaning (yrs)	Period of independent growth, α (yrs)	Weaning wt/adult wt, δ	Annual fecundity, b (daughters/yr)	αb	αM
Human[a]	32.9	17.3	2.8	14.5	0.21	0.142	2.05	0.44
Orangutan	17.9	14.3	6.0	8.3	0.28	0.060	0.52	0.46
Gorilla	13.9	9.3	3.0	6.3	0.21	0.126	0.79	0.45
Chimpanzee	17.9	13.0	4.8	8.2	0.27	0.087	0.70	0.46

a. Source: reference [100] and references therein. a. Pooled data from Ache and !Kung hunter-gatherers.

3.6   Co-evolution of lactation, weaning and life history

These unusual life history characteristics are of more than passing interest, because they suggest that humans have evolved a phylogenetically distinctive response to the fundamental invariants that predict relations between the life history parameters of extant mammals. [100, 117] Specifically, humans differ from other primates in the way in which we conform to Charnov's model predicting cross-species variation in mammalian life histories.[118-120]

Charnov's model proposes that individual growth rates take the form $dW/dt = AW^{0.75}$, where W is body mass and A is the fundamental parameter referred to as the "production coefficient". A takes a similar dimensionless value within each mammal clade, constrains both the rate of juvenile growth and the rate of maternal investment during gestation and lactation, and so links the life history parameters of individual species. The model divides growth into two periods. In the period from conception to weaning, growth is a function of the mother's size. In the period of independent growth from weaning to maturity (α), however, growth is a function of the individual's own body size.

For a given species, the value of α is selected as an evolutionarily stable strategy that responds to the tradeoff between the fitness benefits of beginning reproducing sooner (i.e. having a greater chance of surviving to reproduce) and the fitness benefits of growing longer (i.e. ability to produce more and/or larger offspring at a larger maternal sizes). Thus, α is a measure of "delayed reproduction", and maturity marks a transition where production previously allocated to growth is reallocated to reproduction. The model predicts that any ecological conditions that decrease adult mortality rate (M) will increase adult lifespan ($1/M$) and select for delayed maturity (i.e. increased α) to reap the fitness benefits of larger size. It also predicts that production subsequently invested in offspring increases with age at maturity,

because it is a function of maternal size (W_α). Thus, the size at which offspring become independent feeders (i.e. are weaned) is proportional to, and constrained by, maternal size.

Several observed cross-species life history correlations fit this model well. First, both α and M vary widely across mammal species, but inversely. In other words, larger species live longer and begin reproducing later, and the product (αM) is approximately invariant. Second, the ratio of size at "independence" to adult body size ($W_o/W_\alpha = \delta$) is approximately constant [55-56]; the relationship is very slightly negative, $R = 0.991$). In other words, weaning weight is constrained by maternal mass (W_α), and size at which offspring are weaned increases in direct proportion to maternal body size. Third, larger, later-maturing species produce larger but fewer offspring. In other words, annual fecundity (the number of daughters produced per year, b) decreases as age at maturity increases with α, and the product (αb) is another approximate invariant. This can be explained by the observation that size at weaning increases faster with maternal size than does the total production that mothers have available to invest (which scales allometrically, $W^{0.75}$, not proportionally).

Primates have a very low A, averaging less than half of that of other mammals (approximately 0.4 vs 1.0). This accounts for their slower growth, lower fecundity for size, and smaller size at a given age of maturity. The ratio of weanling size to adult size, δ, is approximately 0.33 across both mammals in general and primates in particular, but lower in all great apes, and especially low for humans (Table 18-2). In contrast, αb is approximately 1.7 for mammalian taxa in general and for primates, but is less than 1.0 for other great apes. It is exceptionally high (greater than 2.0) for humans.

Compared to other hominins, therefore, humans appear to wean relatively earlier and at relatively small size, to spend longer in "independent" growth before first reproduction, to reproduce at much higher rates during the child bearing years, and to achieve lower adult mortality and longer lifespan. The selective forces that have resulted in such markedly lower δ, higher b, longer α, lower M, and possibly higher value for A require explanation and are currently the subject of intense debate among evolutionary anthropologists. For community nutritionists, the clustering of these anomalous life history traits suggests that shifts in the patterns of exclusive lactation and transitional feeding were intimately involved in the co-evolution of human reproductive scheduling, care giving and dietary practices.

3.7 Complementary feeding

Figure 18-4 presents a model of the evolved pattern of postnatal child feeding reconstructed from current international feeding recommendations

based on a host of clinical studies.[22-23] Initiation of breast-feeding within an hour of birth followed by a 6 month period of exclusive breast-feeding promote optimal growth and development of healthy newborns. Introduction of "complementary foods" (i.e. nutritionally rich and relatively sterile combinations of foods acquired and processed by care givers and fed only to infants and toddlers) is necessary to support increased daily dietary intake after approximately 6 months of age. Family foods (i.e. raw foods and combinations of foods collected, processed and shared by older juveniles and adults) begin to contribute to total dietary intakes during the second half of infancy. During the period of complementary feeding (CF), which continues at least until the third year of life, breast-milk remains an important, sterile source of nutrients and immune protection but complementary and family foods increasingly contribute to total intake as chewing, swallowing and tasting competencies develop. The frequency of suckling and volume of milk consumed diminish gradually, but the age at weaning (d) is extremely variable and there is no upper age limit at which breastfeeding ceases to be of some benefit to children.

This specialised pattern of transitional feeding is unique among primates, and has other corollaries. Detailed studies of the diets and foraging behaviour of non-human primate weanlings are few, but it is clear that provisioning never approaches the levels observed in human populations.[121] Humans are the only primates that wean juveniles before they can forage independently.[91] The targeting and sharing of high yield, nutrient dense foods that entail high acquisition and processing costs is a specialisation of human foragers [122], as is the use of heat treatments and combination of raw foods in "cuisine".[123-124] We are also unusual in the extent to which we recruit and distribute help among conspecifics, including young child feeding and care.[110,125] Indeed, transitional feeding appears to be fundamentally different. Thus, weaning marks a shift to allo-caregiver support, not feeding independence.

The developmental sequence of changes in the physiological characteristics of young children suggests that early childhood evolved in an environment in which the transition to adult foods occurred over several years.[62] Examples include the development of suckling, swallowing and chewing; mechanical changes related to growth of the jaw, the temporo-mandibular joint and tooth eruption; changes in the expression and ratios of gut enzymes and absorption factors associated with the intestinal mucosa; and changes in immunocompetence and renal function. Flexibility in the duration of transitional feeding was likely made possible during the long gathering and hunting phase of human existence by complementary feeding of foods specially collected and processed for the use of infants and young children. Growing human infants outstrip the maternal supply of nutrients at

about 6 months, and may be able to survive without milk at much younger ages and smaller body sizes than do other infant apes. Nevertheless, there is ample evidence to indicate that continued breast-feeding during the period of complementary feeding would have conferred significant fitness benefits for ancestral mothers and babies.
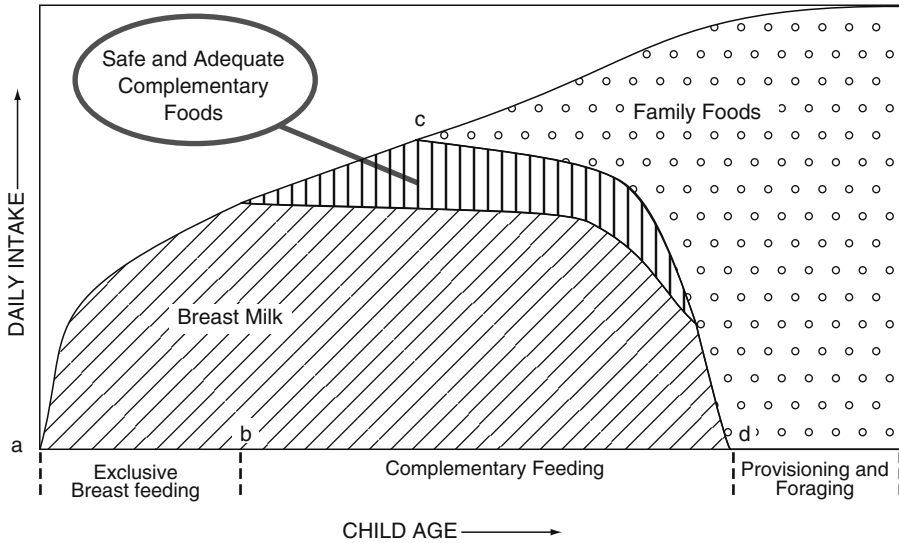

Figure 18-4. Postnatal development of feeding in humans. Key: (a) birth; (b) introduction of complementary foods; (c) introduction of family foods; (d) last suckling. The order of events and phases presented assumes no constraints on maternal and caregiver time allocation or access to food resources and represents an estimate of optimal patterns based on clinical observation. In its general form, we can assume this to be a pattern of care and feeding shaped by natural selection in past environments. Adapted from reference 126**.**

4.   THE COMPLEMENTARY FEEDING HYPOTHESIS

4.1   An evolutionary scenario

How did the behavioural ecology of human lactation come to be so different from that of other mammals, including our closest relatives the apes? We can speculate that the hominid ancestors of modern humans were constrained by similar ecological factors as non-human primates are today.

There would have been a selective advantage to weaning relatively early for body size if the fitness cost to juveniles could have been reduced. There is abundant evidence that human ancestors evolved behavioural strategies for accessing high quality food resources from their habitats. It is plausible to suggest that, some time after the hominid-ape split, the hominids ancestral to humans began to target foraged foods yielding specific key nutrients or to render them more nutritious for weanlings through complex processing. Some of the nutritional constraints on offspring survival and development were thereby relaxed, and new shifts in life history occurred.

First, feeding of older nurslings with nutrient dense, high quality "complementary" foods made possible the reduction of birth intervals without incurring a cost of increased nursling mortality or compromised functional development. Contemporary clinical data showing benefits of improved energy and micronutrient density in the young child's diet suggest the long-term fitness gains for small improvements in ancestral juvenile diets were large. Substitution of self-foraged foods during the juvenile transitional feeding period with complementary foods that more nearly matched infant dietary needs for energy and specific micronutrients therefore provided a dietary mechanism for resolution of the fundamental life history tradeoff between maximising offspring quality or quantity. It resulted in few changes in the composition of breast-milk, and did not diminish the necessity of breast-milk in early infancy.

Second, the behavioural patterns that allowed for the gathering, preparation and sharing of complementary foods for weanlings were "exapted" for the preparation of high quality foods for older, weaned juveniles. Parents who continued to provision offspring for many years after weaning gained a selective advantage. Offspring who evolved to rely on continued feeding of processed, nutrient dense foods rather than on learning to forage raw foods would have benefited from a richer and more reliable food supply during the "independent growth" period, α. Relaxation of ecological pressures to reach adult size quickly selected for extension of a new "childhood" phase in ancestral human development. Continued extension of childhood may have occurred through both later maturation and earlier weaning, and opened a window of opportunity for highly complex social learning.

A third shift in life history may have occurred through consumption of these same foods across the lifespan as "family" foods. Once adults began to prepare and share high quality "family foods" more widely, fitness gains accrued to social group members of all ages.[2] Improvement in maternal diet, and hence birth outcomes and maternal survival, probably produced the strongest selection pressure driving a shift to cooperative foraging and food sharing. Thus, complementary feeding and early weaning triggered and

facilitated the evolution of more general shifts in human foraging, parenting and social behaviour.

The transitional feeding of highly processed foods in addition to breast-milk may be linked to a cluster of derived species characteristics unique to our species that appeared during the last 5-7 M years (Figure 18-5). These include omnivory, social foraging, food processing and sharing, extended childhood, overlapping generations, menopause, fat storage, relatively high reproductive rate and efficient complementary feeding. Life history changes associated with the origin of complementary feeding likely include shorter and more plastic lactation duration, smaller size at weaning, shorter closed birth intervals, and increased weanling survivorship. Other life history changes possibly associated with increasingly efficient complementary feeding probably include shortened exclusive lactation and the evolution of a post-reproductive phase in females.[3]

4.2   Some predictions

This evolutionary scenario is consistent with the patterns of similarity and difference observed for human, non-human primate and mammalian lactation biology. It focuses attention on the fitness benefits of improved nutrition at a critically vulnerable phase in the life history of any primate, the transitional feeding period. It forces us to consider the ways in which the timing and progression to weaning may have been linked to changes in diet and life history among human ancestors. It raises questions about what aspects of the diet are most critical (e.g. which micronutrients) and during what part of the life course the fitness benefits of improved diet would be maximal. It therefore improves upon previous models of the co-evolution of human diet and life history, which too often invoke a rather vaguely defined selective advantage of "improved diet quality".[4]

Drawing upon the salient aspects of this scenario, we can hypothesise that the ability to maintain or increase weanling growth, functional development and survival by substituting moderately processed "adult" foods with nutrient dense, high quality "juvenile" foods was a key adaptive shift among human ancestors. This hypothesis generates several phylogenetic predictions. These are that complementary feeding is: (i) a derived behavioural characteristic, i.e. novel; (ii) universal, i.e. species-typical; (iii) uniquely evolved in the hominin lineage, i.e. a rare adaptation; (iv) recent, i.e. arising since the split with last common ancestor of apes and humans; and (v) co-evolved with diet, life history and "culture". The comparative evidence reviewed suggests these phylogenetic predictions are met.

   The "complementary feeding hypothesis" also makes a series of testable mechanistic predictions about the selective advantages of complementary feeding over ancestral alternatives. These are that the behavioural shift to complementary feeding: (i) resolved tradeoffs and conflicts of interest between ancestral infants and their caregivers over the timing of weaning; (ii) increased maternal fertility; (iii) increased offspring survival; (iv) increased development of offspring functional competence; and (v) favoured a complex suite of dietary adaptations among adults and older juveniles. Although it will be difficult to develop indicators of past fitness differentials with which to test these predictions or to find fossil evidence for when complementary feeding began, future work in paleoecology and paleoanthropology has the potential to throw light on the sequencing of steps in the evolution of complementary feeding in relation to other evolutionary shifts.
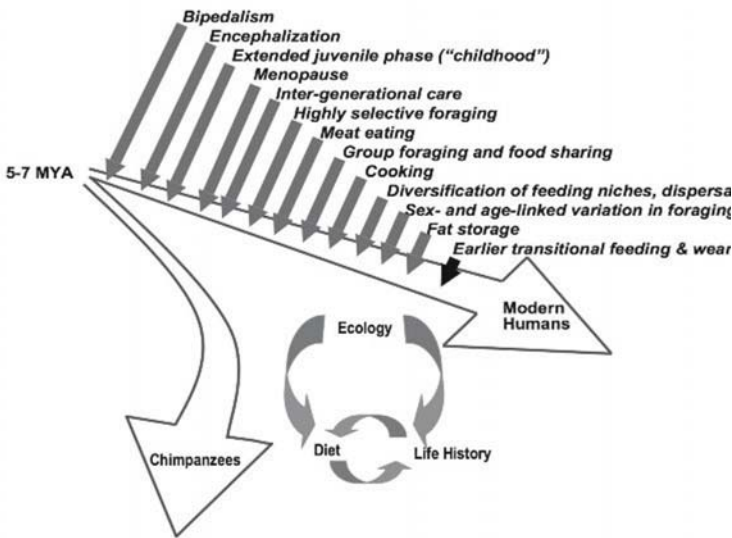
Figure 18-5. Some evolutionarily derived characteristics of human anatomy, behaviour, diet and life history. Any changes in scheduling and fitness consequences of lactation and complementary feeding among hominids must have occurred since the split with the last common ancestor of humans and chimpanzees and co-evolved with significant changes in diet, life history and ecology. Although we know that bipedalism preceded encephalisation, the order and timing of the many evolutionary changes in the human lineage remain poorly understood.

5.   RELEVANCE TO CONTEMPORARY ISSUES

5.1   Untimely complementary feeding

The logic of natural selection leads us to assume that in the distant past complementary feeding and flexible weaning did not compromise survival or functional development of the average infant. Indeed, all evidence suggests these behavioural changes were adaptive and sufficiently beneficial to produce lasting changes in human life history scheduling.

In modern contexts, however, a mismatch between actual and recommended young child feeding practices undermines the health of populations. This mismatch results in part from a tendency for families under certain kinds of constraint to introduce other foods to infant's diets sooner than is optimal for maternal and child health outcomes. Why does this happen?

Part of the explanation is to be found in an evolutionary history of increasing behavioural control over the pattern of lactation. This has given contemporary mothers a range of options for minimising the physiological and opportunity costs of lactation. Unfortunately, in some contexts a strong tendency to reduce the frequency of suckling and the duration of lactation may also result in poor health outcomes for child both children and mothers. The evolved flexibility in human lactation patterns and the wide availability of apparently adequate and convenient breast-milk replacements tend to work against efforts to promote exclusive and continued breast-feeding. The greatest degree of mismatch between recommended and actual practices is observed in industrial societies. These are the societies in which the social and opportunity costs of lactation and the safety, convenience and adequacy of complementary foods and breast-milk substitutes such as infant formula are popularly perceived to be highest.

The problem is not peculiar to industrialised societies, however. In noting that humans exhibit an unusually high degree of variation in weaning age, Hartmann and colleagues warned against the assumption that lactation patterns observed in hunter-gatherer and other "traditional" societies reflect evolved, species typical behaviours that optimise the function of the human breast.[42] Indeed, the central tendency for the *earliest* reported age of introduction of liquid and solid non breast-milk foods falls below 6 months for a sample of subsistence societies with natural fertility (Table 18-2). The earliest reported age at weaning falls below 24 months. There are significant problems with the reliability of the data, and it is not possible to ascertain the proportion of individual children fed according to the recommendations in these populations therefore, Nevertheless, we can infer that breast-feeding

patterns do fall short of the current clinical recommendations for many individual children in subsistence societies.

The agricultural and industrial revolutions are recent innovations on an evolutionary timescale. Contrary to popular assumptions, the adoption of agriculture reduced food security, diet quality and general levels of health for a large proportion of the population.[130-131] It also brought radical changes in the ecology of infant care, particularly the opportunity and social costs of maternal time allocation. Mothers in societies that depend mostly on productive subsistence (i.e. various forms of farming and herding) tend to do work that interferes with frequent breast-feeding.[132] Lactation and complementary feeding patterns therefore concord most closely with global recommendations among foraging (i.e. gathering and hunting) societies (Table 18-2). The mean reported minimum duration of breast-feeding exceeds the WHO minimum only in these populations. Across subsistence societies (most of which actually obtain food from a combination of productive and extractive subsistence strategies), the mean duration of breast-feeding increases significantly with the proportional contribution of hunted foods to the diet (Age = 32 +0.346 [% dependence on hunting], $F_{1, 181}$ = 11.9, p= 0.001).[129] In contrast, caregivers in predominantly farming and herding societies show a tendency towards earlier weaning and untimely introduction of liquid and solid foods (earlier and later than recommended, respectively) (Table 18-2). Nevertheless, the range of variation between subsistence populations in reported child feeding indicators is considerable and these trends are not statistically significant.[129] In summary, untimely complementary feeding is widespread and not easily predicted.

5.2   Promotion of optimal young child feeding

The evolution of complementary feeding and the rise of technology have together rendered human breast-feeding vulnerable to erosion. On the other hand, the fact that our child feeding practices have evolved to be labile should encourage efforts to promote exclusive and continued breast-feeding and safe, timely and adequate complementary feeding. A major challenge for policy makers is how to develop effective methods for promoting such improved young child feeding practices in populations that vary enormously in levels of health risk and other characteristics.[133] The stakes are high because a harsh paradox exists in today's world.[134] While millions survive without ever tasting their mother's milk, many more millions depend on it for a better chance to live. Compared with our foraging ancestors, the differential consequences of infant feeding practices on health and wellbeing signal an increasing divide between the "haves" and the "have-nots" in our species.

In developing country settings, caregivers tend to titrate breast-feeding, complementary feeding and childcare in response to shifts in ecology, subsistence and social environment. Across cultures, underlying attitudes and values about child feeding are often broadly concordant with optimal practice, but caregivers focus more explicitly on tradeoffs between infant/child and maternal/caregiver needs. Cues used to assess the health and development of children and the social and physical constraints on caregivers' ability to provide care or to value investment in children are critical influences on the salient features of young child feeding.[116, 135-137] More often missing are the material conditions conducive for optimal breastfeeding and complementary feeding.

In industrialised nations, the overwhelming evidence that lactation remains a crucial component of a healthy life course for both babies and women who choose to reproduce persuades scientists. Lactation improves life for all, as we can assume it has done for millennia. For some breast-feeding advocates the idea that contemporary humans have the same bodies as those of humans living a foraging existence thousands of years ago is a way to encourage "natural breast-feeding".[138-139] Messages reminding people that mammals are "mothers to us all" are expected to reinforce understandings that breast-feeding is natural and beneficial. Indications that optimal child feeding may have been prevalent in at least a few human societies reassure professionals that they are feasible.[128]

Table 18-2. Comparison of recommended and reported young child feeding indicators for non-industrial populations

Feeding transition:	Clinically recommended age for healthy children (months)[a]	Earliest reported age, months ± SEM (n societies) [b]		
		Pooled	Foragers	Farmers	Herders
Liquid foods introduced	~ 6	3.6 ± 0.9 (18)	- (1)	3.5 ±1.0 (13)	4.7 ±2.6 (4)
Solid foods introduced	~ 6	5.7 ± 0.6 (39)	4.8 ±0.8 (6)	5.5 ±0.8 (29)	7.9 ±2.1 (4)
Weaning from breast	> 24	22.7 ± 0.9 (108)	26.9 ±1.7 (24)	21.1 ±1.1 (72)	23.9 ±2.7 (12)

Sources: a. Reference 127; b. Reanalysis of indicators of age at introduction of complementary foods and termination of breastfeeding from 172 ethnographic and demographic reports published between 1873-1998, following methods in references 128-129.

Beyond the world of lactation researchers and public health practitioners, however, most people think of children as not necessarily needing breast-milk to survive; in many situations they are essentially correct. Many lay people living in such societies now question whether lactation is still useful for humans. It is therefore very important to disseminate new knowledge about the lowered mortality and illness rates among fully breast-fed children in developed and emerging economies. But is also important that this be done in ways that resonate with people's attitude's, beliefs and values and their common sense observations.

The challenge is formidable. For example, there is evidence that use of the "argument from biology" may be counter-productive in the promotion of breast-feeding because some people fear to be stigmatised as "primitive".[139] Breast-feeding is increasingly portrayed in popular culture as a behavioural anachronism that limits opportunities for both mothers and babies, and interferes with their ability to live comfortably in an industrialised and capital-driven society. The breast is no longer regarded as primarily an organ of nutrition, immune defence and fertility regulation. Even some influential pediatricians contend that the technologically fed baby may have more desirable outcomes, rather like a doped athlete. There now exists in most societies a counter-veiling, dominant and popular cultural model that lactation is an artifact of our past, and that breast-feeding, like hunting and gathering, can be improved upon.

To some extent, this kind of shift in cultural thinking is yet another legacy of our success in complementary feeding. The industrial production and commercial marketing of formula companies have played a role in this, but broader cultural forces are at work. Threats to a culture supportive of breast-feeding are ubiquitous and linked with seemingly inevitable shifts in most people's worldview. Such ideas have "gone global" because they reinforce the sense of modernity felt by the growing populations of the world's urban centers. In so far as they contribute to poor health outcomes for infants and mothers, many observers fear such cultural changes may lead inevitably to the erosion of breast-feeding. Everywhere, industrialisation and modernity are associated with the highest prevalence of untimely supplementary feeding and formula feeding. There is no doubt that ongoing changes in culture and technology exert a powerful influence over contemporary patterns of human lactation. The challenge for promotion is not to allow our evolutionary heritage, which has served us well until recently, to undermine the health of our children.

6.   CONCLUSIONS

Comparative biology suggests humans have evolved a uniquely flexible strategy for feeding young. Overall, the costs of human lactation seem especially low. The pattern of postnatal feeding is distinctive. Compared to other mammals, humans tend to have a low weaning weight relative to birthweight and individuals of our species are weaned at a wider range of weights and ages relative to adult body size and age at maturity. The use of both complementary foods and family foods appears to be unique to humans. Nevertheless, the three adaptive advantages of lactation (infant immune protection, infant nutrition, maternal fertility regulation) are retained in humans, and there is no cogent evidence for additional derived features of human milk or mammary glands. Humans need breast-milk for optimal growth and development, just like any other mammal.

Complementary feeding is a species-typical, derived behavioural characteristic that evolved uniquely in a branch of the hominid lineage leading to humans. It probably evolved as a facultative strategy for resolving tradeoffs between maternal costs of lactation and risk of poor infant outcomes. Comparative data are consistent with the hypothesis that complementary feeding is an adaptation that increased maternal fertility by accelerating the transition to weaning without decreasing offspring survivorship. It is plausible that complementary feeding of foods specially collected and processed for the use of infants and young children evolved during the long gathering and hunting phase of hominid existence. Among mammals, only humans have evolved the capacity to keep young alive without consumption of any maternal milk. This biocultural innovation now threatens to erode breast-feeding practice below physiologically healthy and previously adaptive thresholds.

NOTES

1. The term "hominid" refers to a clade of bipedal apes, including Australopithecines and members of the genus Homo, some of which may have been ancestral to modern humans. The wider grouping "hominin" includes the great apes and humans.
2. It is interesting to consider the advent of "fast foods" as merely a recent extension of a general evolutionary trend towards widespread preparation and consumption of highly nutrient-dense meals.
3. Provisioning of descendent kin such as daughters and grandchildren could result in higher fitness returns than continued reproduction. This proposal differs from the version of the "grandmother hypothesis" proposed by Hawkes and colleagues.[140]

4. To date, few anthropologists have called for a focus on hominid strategies to garner foods of special value to weanlings (a rare example is Binford's argument regarding scavenged bone marrow.[141]

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