

# Evolution of Infant and Young Child Feeding: Implications for Contemporary Public Health

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## Key Words

lactation, breastfeeding, weaning, adaptation, primates, phylogeny

## Abstract

Evolutionary anthropological and ethnographic studies are used to develop a general conceptual framework for understanding prehistoric, historic, and contemporary variation in human lactation and complementary feeding patterns. Comparison of similarities and differences in human and nonhuman primate lactation biology suggests humans have evolved an unusually flexible strategy for feeding young. Several lines of indirect evidence are consistent with a hypothesis that complementary feeding evolved as a facultative strategy that provided a unique adaptation for resolving tradeoffs between maternal costs of lactation and risk of poor infant outcomes. This evolved flexibility may have been adaptive in the environments in which humans evolved, but it creates potential for mismatch between optimal and actual feeding practices in many contemporary populations.

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**Complementary foods:** nutritionally rich and relatively sterile combinations of foods acquired and processed by caregivers and fed to breastfed infants and toddlers after about six months of age

## INTRODUCTION

Two observations about the patterns of infant and young child feeding (IYCF) in contemporary human societies are puzzling for nutritionists and anthropologists, respectively. First, the proportion of newborns that breastfeed exclusively for six months, receive timely and appropriate complementary foods, and continue to breastfeed into their third year is small, even though overwhelming evi-

dence suggests such a pattern is optimal for most healthy, term infants (including low-birth-weight infants born at >37 weeks gestation). Second, humans tend to wean their babies significantly earlier than most other apes do, even though children depend on others for subsistence much longer than do the offspring of any other mammal (172). This article reviews zoological, anthropological, and nutritional data that suggest these two apparently paradoxical observations are evolutionarily linked. It summarizes recent conclusions about the unique characteristics of human life history and discusses how they may be related to unique characteristics of human lactation biology. It briefly reviews data on variation in lactation patterns among nonhuman patterns and data on variation in IYCF among preindustrial human societies and ancient populations. The aim is to provide an evolutionary perspective on why optimal IYCF is so rare and difficult to promote in modern human societies that are far removed from the original conditions shaping human adaptation.

## COEVOLUTION OF LIFE HISTORY AND LACTATION BIOLOGY

It is possible to distinguish the evolutionarily derived features of human life history (44) and lactation biology from those that are shared with other mammals by using the comparative methods of zoology and drawing on physiological and epidemiological data that signal an evolved, optimal pattern of human IYCF.

## VARIATION AMONG MAMMALS

Mammals vary in age at weaning, as well as in many other characteristics that together describe their life history (109), such as age at first reproduction, gestation length, interbirth intervals, and age at death. Much of this variation is linked to more or less species-typical patterns of growth and development, and is associated with variation in body size, demography, sociality, and ecology (36, 39, 153, 171,

187). Evolutionary theory suggests life history variation is an adaptive response to natural selection within physiological, ecological, and social constraints (37, 38, 44, 74, 186, 216).

Lactation probably evolved between 210 and 190 million years ago (mya) (20, 41, 91, 127, 145, 147) and prior to the origin of another defining characteristic of mammals, specialized hair and fur (143). Lactation probably evolved initially as an adaptation to transfer immune factors to offspring (99) and later as an adaptation to make efficient use of maternal body fat and other stored nutrients in feeding offspring and spacing births (45, 178, 179).

Significant diversity exists in the species-specific characteristics of lactation biology and their relation to life history (29, 91, 98, 152). Milk immune components (82), milk energy density (169), milk yield (168, 185), relative milk energy yield (152), and milk composition (79) vary among species with disease risk, body size, litter size and mass, maternal diet, maternal use of body stores, suckling patterns, and care behavior. This diversity reflects phylogenetic differences in the selective response to shifts in disease ecology, foraging opportunities, and constraints on growth and development. **Table 1** summarizes some key trends linking variation in lactation biology and life history across mammals.

Nevertheless, all surviving mammals retain lactation as a key adaptation that contributes to the organization of life history characteristics (88). Four basic functions of lactation present as plesiomorphies are summarized in **Table 2**. Also highly conserved are similar mechanisms of lactogenesis (67, 89), mammary development (32), immunological activity (82), milk transport proteins (158), and metabolic adaptation during lactation (228).

## SIMILARITIES AMONG NONHUMAN PRIMATES

More is known about the range of life history variation observed among nonhuman

**Table 1 Key trends linking variation in lactation biology and life history across mammals**

|   |
|---|
| 1. Marsupials commonly overlap lactation with gestation of younger offspring, whereas most placental species do not.  |
| 2. The period between first solid food consumption and weaning is long in species with single, precocial young, and provisioning may occur, whereas first solid food is usually eaten near weaning in polytalous species with altricial young (98). |
| 3. Milk energy concentration decreases with maternal and neonatal size.   |
| 4. Milk fat and protein concentration are positively correlated, and both are negatively correlated with sugar, which is associated with suckling frequency.  |
| 5. Milk energy output at peak lactation scales with basal metabolic rate according to Kleiber's Law.  |

primates and hominids (40, 80, 92, 93, 140, 141, 176, 211–214, 227) than about variation in primate lactation biology (204, 242).

## Life History

Recent work suggests the common ancestor of primates weighed between 1 and 15 g and therefore had high metabolic, reproductive, and predation rates, and that body size remained below 50 g during the early Eocene primate radiations (78). Extant primates, however, range in size by an order of magnitude (92). Compared with other mammals, they are characterized by a slow life history and low postnatal growth rates (40, 92, 93). The few available data on variation in primate lactation biology suggest all species share common adaptations to meet infant nutritional needs conditioned by this characteristically slow life history.

**Life history:** the temporal organization of major biological events over the lifetime of individuals. Life history theory aims to explain why life cycles vary among species and individuals

**Lactation:** the ability to secrete immunologically active and nutritious milk from ventral epidermal glands; a defining characteristic of mammals

**Table 2 Basic functions of lactation present in all extant mammal species**

|   |
|---|
| 1. Transfer protective functions of fully developed immune system across generations.               |
| 2. Optimize litter size to allow titration of maternal investment across sib sets.                  |
| 3. Facilitate efficient reproduction in unpredictable environments lacking special foods for young. |
| 4. Increase behavioral flexibility and opportunities for learning.                                  |

**Weaning:** the termination of suckling. Weaning is a uniquely mammalian life history marker that may or may not be preceded by a period of feeding on other foods in addition to mother's milk

**Plesiomorphies:** shared primitive characteristics no older than the last common ancestor of a phylogenetic group of organisms

**Exclusive suckling:** a life history phase during which a juvenile mammal derives all nutrients from maternal milk. It is often referred to as "infancy" in nonhuman mammals

**Transitional feeding:** a life history phase during which nutrition is derived from a combination of maternal milk and other foods foraged by the infant, its parents, or others. It is poorly described for most primates

## Milk Composition

Most previous reviews conclude that the gross composition of milk does not vary widely across nonhuman primate species with differences in body size, reproductive rates, patterns of maternal care, or other life history characteristics (32, 57, 69, 117, 173, 180). A single recent study reports variation in milk protein within a species in relation to parasitic infection (108). Primates are unusual among mammals because the milk they produce is lower in volume, more dilute, lower in energy, fat, and protein, and higher in lactose than would be predicted by body size (152), and because length of lactation is relatively long and always exceeds that of gestation (91).

It has long been hypothesized that these shared characteristics of primate milk coevolved with low reproductive rates and slow life histories relative to body size (15, 138, 167). Thus, a lower protein concentration of primate milks coevolved with slower growth rates (168, 169); lower fat concentration coevolved with the behavioral ecology of continuous infant carrying (which facilitates frequent suckling and is unusual in any other order of mammals) (15, 152, 170, 220); and a relatively high lactose content coevolved with the lower fat storage in adult females and low fat content of milk, and may also be linked to faster rates of postnatal brain growth. There is, however, no evidence that levels of long-chain polyunsaturated fatty acids (LCPUFAs) increase among primates with rates of postnatal brain growth (192).

## Juvenile Feeding Ecology

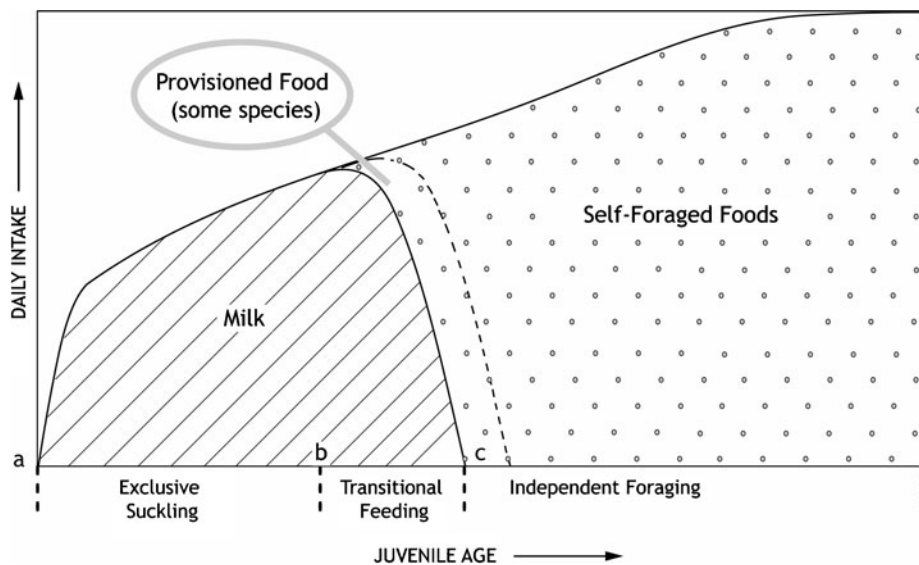
One correlate of a relatively slow life history is the relatively slow development and early maturation of the gastrointestinal tract in primates (195). This means that there is little clustering of gut maturational changes around the species-typical age at birth and age at weaning. Primates are therefore able to begin consuming milk even if born preterm and are generally viable from about 70%

of the length of gestation without intensive neonatal care.

Nevertheless, from a nutritional perspective, nonhuman primate postnatal life can be divided into three phases (exclusive suckling, transitional feeding, and weanling) separated by two key life history markers (first consumption of solid food and weaning) that can be used to define two life history variables (age at first solid food and age at weaning) that increase with body size. Thus, nonhuman primates conform to a generalized mammalian pattern linking life history to feeding ecology (**Figure 1**). Juvenile daily intake of energy and specific nutrients increases from birth and is entirely due to greater milk intake during exclusive suckling. After weaning, further increase in total intake occurs by means of independent foraging or maternal provisioning.

## Transitional Feeding

Variation in transitional feeding has yet to be fully described and explained and may be substantial both within and between species (136–138). There are few data with which to assess the length of transitional feeding in primates or the relative nutritional contribution of milk versus foraged foods (205). It has been hypothesized that relative length of transitional feeding is inversely related to adult diet quality (205), but available data are insufficient properly to test this. In the absence of good observational data it has been generally assumed that nonhuman primate infants wean relatively abruptly and begin to forage on foods similar to those selected by the mother, processing them largely for themselves. However, the transition to weaning is a gradual process in at least one ape, the orangutan (226), and possibly chimpanzees (165). Similarly, although it is commonly assumed that parental provisioning of juveniles is rare or absent in most species (75, 114, 122), there is limited evidence that it occurs in apes (166).



**Figure 1**  
Key nutrition-related life history phases and markers for a generalized mammal.

## Weaning

Last suckling is very difficult to observe directly in the wild, but captive data indicate that nonhuman primate weaning age is scaled to other life history traits, such as gestation length (92), birth weight (133, p. 245; 139), and adult weight (40), and developmental events such as age at molar eruption (193, 211, 212). However, such traits do not reliably predict age at weaning for all primate species, suggesting that age at weaning is labile. Studies of nonhuman primate behavioral ecology suggest that weaning age is plastic in most species and sensitive to ecological factors that constrain maternal ability to meet the increasing energy needs of growing offspring and the ability of infants to survive without mother's milk (4, 5, 136, 137, 139).

## Infant Requirements

Few data are available on age-specific changes in energy requirements of nonhuman primates, of the total energy costs of growth and maintenance during infancy, or of the proportion met by milk consumed. Observation of ad libitum intakes among several captive large bodied cercopithecine species yields estimates of average infant energy requirements

in the range 0.837–1.255 MJ/kg/d (160, 163). Such intakes are likely to differ from either average requirements or usual intakes in the wild, however. A study of free-living yearling baboons (*Papio cynocephalus*) estimated minimum total energy requirements for growth and maintenance at 0.871 MJ/d, or 0.383 MJ/kg/d (8).

It is difficult to identify studies that estimate the concentration of key nutrients such as vitamin A, vitamin D, iodine, calcium, and essential LCPUFAs in the milk of nonhuman primates (180). At present few conclusions can be drawn for any species about how milk nutrient content varies with maternal diet or about the extent to which exclusive suckling and milk consumption during transitional feeding satisfy age-specific nutrient requirements. Although evolved associations between feeding ecology and milk composition might be predicted across species, the data are too scant to test nutritional ecological hypotheses. For example, it is not known whether primate species that are nocturnal or obligatory carnivores (such as tarsiers) secrete milk richer in vitamin D levels in their milk as they are (no sun exposure) and are similar to felids. The milk of diurnal monkeys and apes is not reported as a rich source of vitamin D,

**Weanling:** a life history phase during which a recently weaned juvenile mammal must forage for itself and subsist on foods similar or identical to those selected by adults

**Synapomorphic:** evolutionarily derived or specialized characteristics shared only by one phylogenetic group of organisms

and it is currently assumed that this is because endogenous synthesis satisfies requirement.

## Maternal Costs

Relatively little is known about the reproductive ecology of wild nonhuman primate mothers. Evidence that they can accommodate the costs of protecting their infants against fluctuations in milk volume and composition when conditions are adverse is scant (57).

It is also unclear to what extent nonhuman primates share a capacity for maternal accommodation of lactation performance in response to moderate decreases in maternal energy or nutrient intakes. Free-living yearling baboons are estimated to consume 2.251 MJ/d, of which approximately 40% (0.900 MJ/d) comes from milk, suggesting their mothers bear the cost of minimal energy requirement (8).

Available data indicate that lactation places a significant metabolic demand on mothers and that limited mechanisms exist to accommodate this (6, 7, 57, 86, 135). Field observations of several species indicate that lactating females increase their intake of high-energy foods (27), overall food energy (196, 215), and time allocated to foraging (4, 58), particularly when forage quality is poor (59). Indirect evidence from captive studies suggests that in some species, energetic costs of lactation are accommodated by energy-sparing adaptations, physiological adaptations (17, 191), reductions in physical activity (17, 87), and shared care of infants (219, 242). No studies have shown conclusively that lactating nonhuman primate mothers are able to reduce the daily costs of milk production using fat stored during pregnancy.

## Maternal Reproductive Ecology

Among wild great apes, female reproductive biology seems designed to avoid conception under food stress rather than to protect mothers from nutritional deficiency during lactation. Lactation, nutritional intake, en-

ergy expenditure, and net energy balance appear to be key influences on fecundity (16, 164). Field observations indicate conception is more likely to occur during periods of positive maternal energy balance because food availability is so unpredictable that conception cannot be timed so that birth will occur during periods of highest food availability (122).

## DERIVED CHARACTERISTICS OF HUMANS

**Table 3** summarizes some key differences in life history parameters among the great ape species, using values obtained for wild apes and hunter-gatherers with natural fertility. **Table 4** summarizes the shared and derived characteristics of human lactation biology.

## Life History

There has been considerable debate about whether and why human life history differs from the typical primate pattern (25, 28, 77, 97, 105, 107, 119, 148, 229, 230, 239). A consensus has recently emerged that, in comparison to other primates, humans have evolved four distinctive life history traits: slow maturation, long lifespans with slow aging, postmenopausal longevity, and weaning before independent feeding (95).

Although not the largest living ape, humans have the slowest life history. This is evidenced by a markedly later age at maturity (marked by age at first birth), a longer period of nutritionally "independent" growth between weaning and maturity, longer maximum lifespan, and longer potential adult lifespan. Not all aspects of human life history are slowed, however. Duration of gestation is similar for all living ape species despite appreciable variation in size at maturity.

Healthy human neonates are relatively large for gestational age and relative to maternal body size, indicating faster fetal growth rates. Estimates of human weaning

age and relative weaning weight are at the short end of the range for great apes.

Most striking, human birth interval is exceptionally short, both in absolute time and relative to body size. Average birth intervals rarely exceed four years in human populations without effective technological means of controlling fertility (232). In marked contrast, half of all randomly selected closed birth intervals exceed four, five, and eight years in wild gorillas, chimpanzees, and orangutans, respectively (75). Since fertility ends at similar ages in human and chimpanzee females, the “species-typical” rate of human reproduction is higher (25).

## Milk Composition

A recent review (205) suggested that humans have retained a number of features of lactation biology that are plesiomorphic with mammals and synapomorphic with nonhuman primates. These shared characteristics include the four basic functions of lactation, similar spectra for the immune components of milk (82), and similar features of gross milk composition (22, 115, 117, 161, 167, 173). These design similarities are likely linked to recurring patterns of pathogen exposure, dietary ecology, and constraints on growth and development that shaped the adaptive radiation of primates. They must have been present in our last common ancestor with apes (which lived approximately 6–7 mya) and in all subsequent hominid species including those ancestral to humans (i.e., various members of the genera *Ardipithecus*, *Australopithecus*, and *Homo*).

Thus, all evidence suggests that the basic composition of human milk, its basic functions in the infant, and its mechanism of secretion and delivery remained unchanged during seven million years of human evolution. This is striking given that during this period there occurred a shift to bipedal locomotion, radical dental and cranial adaptations to a more omnivorous diet, a large increase in brain size, a doubling of adult body size, an even larger increase in the length of the juvenile period

**Table 3 Phylogenetic relationships of great ape species and average values for selected life history parameters (adapted from sources cited in Reference 193)**

|  | Estimated time of divergence from hominid lineage, mya | Adult female weight (range), kg | Gestation length, years | Birth interval, years | Age at weaning, years | Age at first birth, years | Maximum lifespan, years | Period of independent growth, years | Potential adult lifespan, years | Neonate weight/maternal weight, % | Weaning weight/maternal weight, % |
|--|--|---------------------------------|-------------------------|-----------------------|-----------------------|---------------------------|-------------------------|-------------------------------------|---------------------------------|-----------------------------------|-----------------------------------|
| Human, <i>Homo sapiens</i>                               | –  | 47.0 (38–56)                    | 0.7                     | 3.7                   | 2.8                   | 19.5                      | 85.0                    | 16.7                                | 65.5                            | 5.9                               | 0.21                              |
| Chimpanzee, <i>Pan paniscus</i>                          | 5–7  | 35.0 (25–45)                    | 0.6                     | 5.5                   | 4.5                   | 13.3                      | 53.4                    | 8.8                                 | 40.1                            | 5.4                               | 0.27                              |
| <i>Pan troglodytes</i>                                   |  |                                 |                         |                       |                       |                           |                         |                                     |                                 |                                   |                                   |
| Bonobo <i>Pan paniscus</i>                               | 5–7  | 33.0 (27–39)                    | 0.7                     | 6.3                   | –                     | 14.2                      | 50.0                    | –                                   | 35.8                            | 4.2                               |                                   |
| Gorilla, <i>Gorilla gorilla</i>                          | 6–8  | 84.5 (71–98)                    | 0.7                     | 4.4                   | 2.8                   | 10.0                      | 54.0                    | 7.2                                 | 44.0                            | 2.3                               | 0.21                              |
| Orangutan, <i>Pongo pygmaeus</i> and <i>Pongo abelii</i> | 12–15  | 36.0                            | 0.7                     | 8.1                   | 7.0                   | 15.6                      | 58.7                    | 8.6                                 | 43.1                            | 4.3                               | 0.28                              |

**Table 4** Summary of shared and derived characteristics of human lactation biology

|   | Plesiomorphic<br>Shared with other<br>mammals | Symplesiomorphic<br>Shared with other<br>primates | Apomorphic<br>Unique to<br>humans |
|---|---|---|-----------------------------------|
| Postnatal immune defense  | X   |   |                                   |
| Optimal postnatal nutrition   | X   |   |                                   |
| Fertility regulation  | X   |   |                                   |
| Developmental window for learning   | X   |   |                                   |
| A period of exclusive lactation yields optimal benefits to mothers and offspring  | X   |   |                                   |
| Low protein and fat and high lactose milk content                                 |   | X   |                                   |
| Frequent suckling, high cost of infant carrying                                   |   | X   |                                   |
| Slow infant growth  |   | X   |                                   |
| A period of transitional feeding yields optimal benefits to mothers and offspring |   | ?   |                                   |
| Age at weaning highly labile relative to other life history traits                |   | ?   |                                   |
| Complementary feeding   |   |   | X                                 |
| Increased plasticity in length of lactation relative to body size                 |   |   | X                                 |
| Reduced infant energy needs   |   |   | ?                                 |
| Significant buffering of lactation by fat storage in pregnancy                    |   |   | ?                                 |

and of total lifespan, a shortening of birth intervals, and an increase in female postreproductive lifespan.

### Juvenile Feeding Ecology

Current international recommendations (49–51, 55, 234, 237) based on clinical and epidemiological data (31, 49, 52, 125) provide a compelling model for the evolved pattern of human IYCF practices because they are predictive of optimal growth and development of healthy newborn humans in favorable environments (76, 202, 204). By this reasoning, the evolved template for human IYCF includes (*a*) initiation of breastfeeding within an hour of birth; (*b*) a period of exclusive breastfeeding followed by introduction of nutrient-rich and pathogen-poor complementary foods at about six months of infant age; (*c*) introduction of high-quality family foods, usually prepared from a variety of raw sources using some form of processing, heat

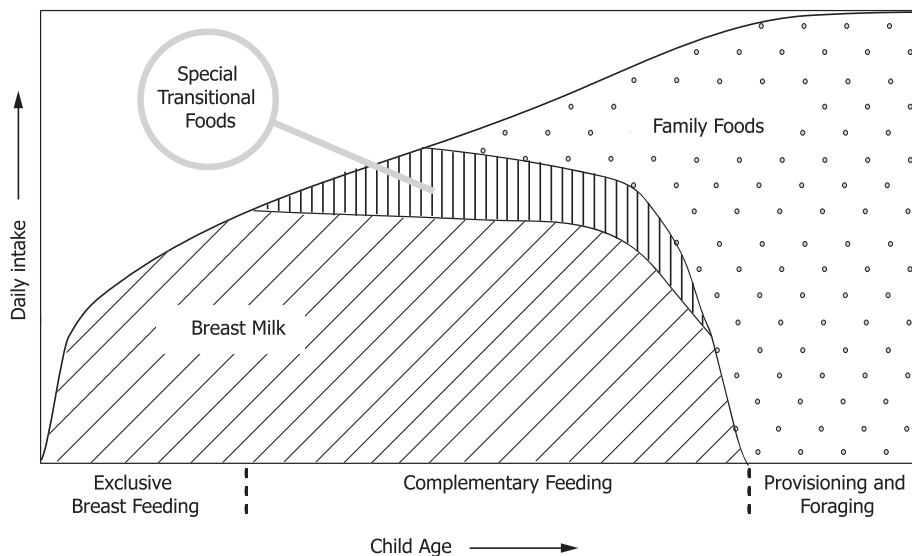
treatment, and mixing; (*d*) continued breast-feeding at least until the third year; and (*e*) a package of “responsive caregiving” throughout the period of nutritional dependency but particularly during the transition to complementary feeding. This evolved human pattern is based on what is optimal for the child in terms of clinical outcomes and is schematized in **Figure 2**. Comparison of **Figures 1** and **2** suggests that important apomorphic features of human lactation biology include (*a*) complementary feeding and (*b*) early and flexible weaning (i.e., increased plasticity in the length of lactation).

### Complementary Feeding

The most remarkable change is the human use of complementary foods, which is unique among mammals (122) and results in a pattern of transitional feeding that appears to be fundamentally different from that of other primates.

**Apomorphic features:** derived characteristics that are not shared with an organism’s ancestors and therefore are likely to be specialized and recent adaptations

**Family foods:** raw foods and combinations of foods collected, processed, and shared by older juveniles and adults and consumed by older members of the family



**Figure 2**

Key nutrition-related life history phases and markers for humans, optimal for infants and young children.

Overwhelming clinical and epidemiological evidence demonstrates that infants have not evolved to make efficient use of other foods before six months (53, 54, 126) and may suffer deficits and increased morbidity if not exclusively breastfed (42, 125). A wealth of data on the trajectory of infant development of feeding competency and changes in the nutritional needs of growing infants in relation to maternal milk supply supports the hypothesis that humans evolved to begin consuming complementary foods at approximately six months of age (205).

After approximately six months of age, complementary and family foods (235) increasingly contribute to the diet (131), as chewing (210, 211, 217), tasting (14, 47, 142), and digestive (134, 194) competencies develop. Frequency of suckling and volume of milk consumed do not necessarily diminish after six months in healthy babies, and the complementary feeding phase continues at least until the third year of life, during which breast milk remains an important, relatively sterile source of nutrients and immune protection.

Ethnographic evidence from preindustrial societies indicates that the duration of exclusive breastfeeding is extremely variable (201). Some indicators suggest that the age-

related pattern for introduction of complementary foods in preindustrial societies concords loosely with the current clinical recommendations for normal, healthy children (203). The modal age of introduction of liquid and solid foods in a sample of published ethnographic reports was six months, suggesting a sizeable proportion of infants in these populations may have been exclusively breastfed for six months.

### Early and Flexible Weaning

Humans are the only primates that wean juveniles before they can forage independently (94). The targeting and sharing of high-yield, nutrient-dense foods that entail high acquisition and processing costs is a specialization of human foragers (18), as is the use of heat treatments and combination of raw foods in “cuisine” (43, 240). We are also unusual in the extent to which we recruit and distribute help among conspecifics, including young child feeding and care (23, 221). Thus, weaning marks a shift to allo-caregiver support, not feeding independence.

Given the potential flexibility and observed variation in weaning age, it is difficult to conclude that humans have evolved

a species-specific, global optimum weaning age. The clinical model suggests that there is no upper age limit at which breastfeeding ceases to be of some benefit to children (66, 151). Current international recommendations are based on evidence that infants benefit from breastfeeding into the third year (238). Continued breastfeeding must have remained a strongly selected component of ancestral maternal strategies because of its powerful anti-infective properties (100, 128, 157) and nutritional or physiological benefits to infants (19, 46) and mothers (10, 129, 223, 224).

The degree of flexibility in age at weaning is unusual among primates and probably a distinctive, derived characteristic. The diversity in human breastfeeding and complementary feeding patterns has long been a focus of lactation researchers (91). The duration of human lactation, if initiated at all, ranges from a few hours to more than five years in recent and contemporary societies (48, 121, 201, 202, 218). This spans most of the range observed for all other species of mammal (90). Ethnographic evidence from recent and contemporary foraging populations indicates that human weaning age is extremely variable within and between groups and that the process of weaning could be gradual (73, 123) or (less commonly) abrupt (71, 72). Humans also wean over a wide range of infant sizes; even among hunter-gatherers human infants are weaned after relatively smaller postnatal weight gain (11).

Nevertheless, some indicators suggest that the age-related pattern for termination of breastfeeding concords with the current clinical recommendations for normal, healthy children. It is estimated that breastfeeding beyond two years was the norm in between 75% (162) and 83% (12) of small-scale societies and that the modal age at weaning was approximately 30 months (201, 203). This suggests a sizeable proportion of infants in these populations may have been partially breastfed for more than two years, a pattern known to be optimal for growth and development. Rigorously collected data from hunter-gatherer

populations suggest mean weaning age of 2.8 years (9). Even if we accept that the latest reliable estimate of modal age of weaning reported [four years among the !Kung (124)] is an indication of a species-typical value, it is well below the five to seven years predicted for primates with our life history parameters (48).

Archaeologists and skeletal biologists have made recent progress in developing approaches to estimating the timing of the trophic shifts associated with complementary feeding and weaning. Their studies use isotopic ratios in bony remains from juvenile and adult skeletons (21, 60, 197–200) and estimate childhood diet from tooth enamel recovered from adult remains (102, 120, 159). Results of such studies show that children in past populations often shifted to solid foods before two years of age while continuing to breastfeed.

## Infant Energy Requirements

Cumulative energy requirements for male babies average 374.2 MJ between birth and 6 months and 959.4 MJ between birth and 12 months (data recalculated from data in Reference 34). Depending on age and sex, estimated mean total energy requirements for growth and maintenance in the first year range between 0.351 and 0.372 MJ/kg/d (1.347 and 3.519 MJ/d). These estimates are regarded as universally valid because healthy infants from different geographic areas show relative uniformity of growth, behavior, and physical activity (33, 76). They fall below the estimates for free-living yearling baboons (8) and well below those for captive large-bodied cercopithecines (160, 163). Thus, although comparative data are scant, human infants appear to have low energy requirements in comparison with other primates. This is likely due to comparatively slower growth.

## Maternal Energy Cost

Human peak milk volume corresponds to a mean infant energy intake of 2.87 MJ/d

(183), which is well in excess of healthy infant requirements in the first six months. The crude energetic costs of human lactation estimated from measurements of daily milk intake among predominantly breastfed infants observed for two years postpartum is  $\sim 1686$  MJ, more than half of which is borne in the first year of infant life (recalculated from data in Reference 183). This corresponds to a mean daily additional cost of approximately 2.3 MJ/d [actually 2.7 MJ/d in the first six months (183)]. Thus, the daily cost of lactation is potentially high ( $\sim 25\%$ – $30\%$ ) in a mother compared with average total energy expenditure for a moderately active nonpregnant, nonlactating woman of average size (calculated from equations in Reference 70). However, two mechanisms allow mothers to accommodate the cost of lactation, both of which appear to be derived for humans relative to our nonhuman primate ancestors.

First, depletion of the maternal fat laid down before and during pregnancy has the potential to subsidize lactation by  $\sim 118.6$  MJ ( $0.325$  MJ/d) in the first year. Fat storage demands the largest proportion ( $\sim 71\%$ ) of additional energy needed to sustain a healthy pregnancy in nonchronically energy-deficient women (62, 132, 183). Nevertheless, reductions in basal metabolic rates and physical activity (61, 183) ensure that for many women average daily costs of pregnancy ( $\sim 0.7$  MJ/d) are low ( $\sim 8\%$ ) in relation to the usual dietary energy intakes and requirements of healthy nonpregnant, nonlactating women ( $\sim 8.78$  MJ/d). In favorable conditions, the average woman begins lactation with approximately 125 MJ of additional fat accumulated during pregnancy.

Second, feeding of nursing infants using safe and nutritionally adequate complementary foods can result in maternal energy savings of almost 1.8 MJ/d in the first year.

Together, healthy fat depletion and complementary feeding reduce the actual cost of lactation estimated to satisfy infant and young child needs for two years by 1023.6 MJ, or

almost 61%. On a daily basis this reduces the net additional costs from  $\sim 2.3$  MJ/d to  $\sim 0.9$  MJ/d. For many women, this represents between 10% and 20% of usual total energy expenditure. Healthy people unconstrained in their access to food or choice of activities can comfortably increase energy intake, decrease physical activity, or both to accommodate increases in daily energy requirement of up to 30%. Despite these adaptations, however, the average daily energetic cost of human lactation is potentially higher than that of pregnancy ( $\sim 2.3$  MJ/d versus  $\sim 0.7$  MJ/d).

One corollary is that human lactation performance is well buffered from fluctuations in maternal condition and nutrient supply (3, 112, 113, 181, 189). Aerobic exercise and gradual weight loss have no adverse impact on milk volume or composition, infant milk intake, infant growth, or other metabolic parameters (56, 144, 154, 155). A single intervention study has suggested that milk production can be improved by maternal food supplementation during exclusive lactation (83). However, most studies suggest lactation is rarely compromised even when mothers are multiparous, marginally undernourished, engaged in high levels of physical activity, and lose weight and fat with age and by season (1, 30, 146, 182, 184, 231).

## Maternal Reproductive Ecology

Lactation, nutritional intake, energy expenditure, and net energy balance are the key influences on fecundity among humans (64, 65, 233). Reproductive endocrinology responds adaptively to maternal nutrient flux and behavioral ecology to schedule reproductive effort across the life span. Flexibility in weaning age reflects an evolved maternal capacity to vary reproduction in relation to ecology (23, 35, 63), the availability of alternate caregivers (110, 123, 150), and other environmental and social factors affecting the costs and benefits of weaning to mothers and infants (156). It has been hypothesized that the maternal cost of reproduction has likely been reduced in

humans by the increased availability of help from older offspring [linked to the evolution of long childhood (24, 26)] and grandparents and other elders [linked to the evolution of greater longevity and vigorous postreproductive lifespan in females (96, 174)]. Observation in contemporary human societies shows lactation behavior is sensitive to maternal workload and the availability of cooperative childcare and feeding (13, 203). Weaning age is later among foragers than among subsistence herders and farmers (207), among whom women often do more of the kind of work that separates them from their infants for extended periods.

## DEMOGRAPHIC IMPLICATIONS

The early age at weaning suggests that ancestral humans evolved an unusual capacity to reduce the length of exclusive and transitional feeding without increasing mortality. In humans, an inverse relationship between birth interval and child survival is mediated by breastfeeding (149, 209, 236). Birth intervals below two years are risky for older sibs. Nevertheless, as a species we are particularly good at keeping young alive in a peculiarly wide range of habitats. Infant and weanling survival is much greater among human foragers [60%–70% (103, 130)] than among apes [25%–50% (106, 107, 121)], and greater still in nonindustrial herding and farming economies (103, 104, 118, 164, 206). These simple demographic differences, which are based in part on differences in juvenile feeding ecology, have had enormous impact. The human population now exceeds six billion, whereas total populations of great ape species are estimated in the low thousands (122).

Shortened birth interval is currently regarded by anthropologists as one of the most evolutionarily significant human deviations from the expected pattern of great ape life history (75, 121, 122, 193, 204). Among our female ancestors, shortening of the periods of exclusive lactation or transitional feeding, or both, likely reduced birth intervals (by accel-

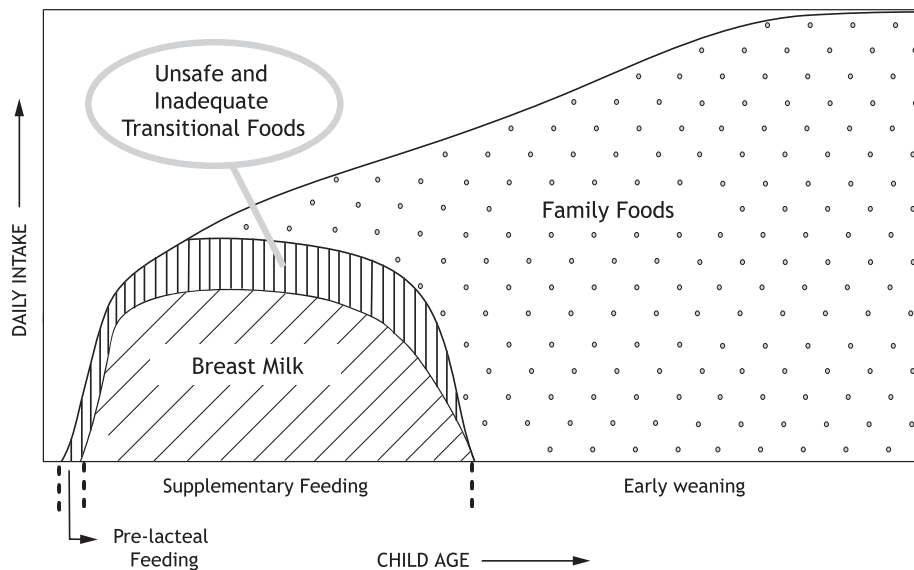
erating the return of ovarian cycling) and may have improved subsequent birth outcomes (by reducing maternal depletion). Shortened birth spacing would have increased maternal fitness only if it did not increase offspring mortality. Reduced juvenile mortality could be achieved only if many of the nutritional components of breast milk were provided by other kinds of foods or if infant development were accelerated so that the period of nutritional dependency was shortened (68, 85, 175).

## IMPLICATIONS FOR CONTEMPORARY PUBLIC HEALTH

Despite burgeoning biomedical (81) and anthropological (225) research on human lactation in recent decades, few scholars have asked broader evolutionary questions about which characteristics of human lactation biology reflect evolutionarily conserved design features and which aspects, if any, reflect a distinctively human phenotype (204, 241). An evolutionary perspective provides insight into why contemporary patterns of IYCF often deviate from the optimal pattern indicated by clinical and epidemiological evidence. Human mothers are physiologically and behaviorally adapted to exercise more choice in the patterns and duration of full and partial breastfeeding than do other primates.

The evolution of the use of complementary foods to facilitate physiologically appropriate early weaning relative to other species has created potential for physiologically inappropriate early weaning and introduction of foods that are not complementary for breastfed infants. One recent and powerful manifestation of this potential is the development and widespread use of commercial infant formulas that meet some of the nutritional needs but none of the immunological needs of infants.

Contemporary human caregivers tend to titrate breastfeeding, complementary feeding, and child care in response to shifts in



**Figure 3**  
Commonly observed pattern of infant and young child feeding, not optimal for child outcomes.

ecology, subsistence, and social environment. Across cultures, underlying attitudes and values about child feeding are often broadly concordant with optimal practice, but focus more explicitly on tradeoffs between infant/child and maternal/caregiver needs. More often missing are the material conditions conducive for optimal breastfeeding and complementary feeding. Mismatch between optimal and actual infant feeding practices in contemporary populations is widespread and presents a major public health challenge (111, 188, 208, 222). Common practices such as discarding of colostrum (84, 190), use of prelacteal feeds (2, 177), reduced breast milk intake due to early introduction of formula and other substances, and early weaning (101) are associated with infant illness and death (116). These suboptimal practices are schematized in **Figure 3**.

## CONCLUSION

Unlike other species, the life histories of mammals have coevolved with the special adaptive advantages and physiological demands of lactation biology. This review has suggested that human patterns of lactation and complementary feeding are intimately linked with the evolution of a distinctive set of

human life history variables. Complementary feeding and fat storage in pregnancy probably evolved in the past 5–7 million years as unique and important human adaptations that together reduce the energetic and opportunity costs of lactation for mothers and the potential fitness costs of relatively early transitional feeding and weaning for infants and young children. The human lactation span is comparatively short. The lower bound for safe complementary feeding has been set at around six months for normal-term and preterm babies by constraints on the evolution of physiological factors such as the growth and maturation of infant systems affecting immune, feeding, and digestive competency. The upper bound for safe weaning has been set above two years of infant age by similar constraints, but the evolution of complementary feeding, together with many other distinctively human evolutionary changes, has introduced enormous behavioral flexibility in maternal response to social and ecological constraints.

This evolutionary perspective provides insight into why, in today's world, young child feeding practices are clinically suboptimal for most children and their mothers, and why many people in both rich and poor societies

fail to adopt recommended feeding practices. Understanding the ultimate evolutionary causes of human variability in young child feeding can provide insights on the proximate causes of patterns of breastfeeding and com-

plementary feeding that subsequently lead to poor health outcomes for mothers and babies. Such insight may help in the design of interventions to promote improved infant feeding practices.

### SUMMARY POINTS

1. Human use of highly processed, nutrient-rich, complementary foods is hypothesized as unique among primates.
2. Complementary feeding is an evolutionarily derived (i.e. apomorphic) species characteristic that coevolved with changes in life history and physiology that reduce the maternal costs of lactation and with distinctive patterns of human foraging, parenting, social behavior, growth, and development.
3. The evolution of complementary feeding occurred because it made exclusive lactation relatively shorter and reduced birth intervals without increasing maternal or infant mortality.
4. Behavioral and physiological shifts during the evolution of complementary feeding enabled human infants to survive without breast milk at a relatively younger age and at a smaller size than infant apes.
5. Contemporary public health challenges arising from this evolutionary history include a strong behavioral tendency among humans to reduce the length of exclusive breastfeeding beyond the lower bounds consistent with optimal infant outcomes.

### FUTURE ISSUES

The following issues have not yet been resolved:

1. The extent of behavioral and physiological variation in the timing and dietary impact of transitional feeding in nonhuman primates and its socioecological correlates (such as quality of adult diet).
2. The absolute timing of steps in the evolution of complementary feeding and the relation of these steps to other key derived human characteristics (such as the origins and maintenance of bipedal locomotion, increased brain size, reduced sexual dimorphism, tool use, food sharing, cooking, and allo-parenting).
3. How humans evolved to overcome the physiological and psychosocial challenges to successful establishment of exclusive breastfeeding that are observed in contemporary populations.
4. How humans evolved to meet the complex challenge of introducing appropriate complementary foods in a timely manner while satisfying other demands on caregivers.
5. How human lactation biology evolved to protect low-birth-weight and premature infants, and to reduce the risks of maternal-to-child transmission of pathogens.

## LINK

<http://www.who.int/child-adolescent-health/NUTRITION/infant.htm>

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## Errata

An online log of corrections to *Annual Review of Nutrition* chapters (if any, 1997 to the present) may be found at  
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