

The Evolution of the Patterning of Human Lactation: a Comparative Perspective

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Some four decades ago, Jeanne Altmann started her detailed field studies of baboon mothers and their infants with a focus on the behavioral ecology of maternal reproductive investment.¹ Around the same time, Sarah Hrdy studied langur mothers and their infants, focusing on the influence of the social environment on a female's reproductive options and decisions.² Their pioneering work has inspired many subsequent studies of female primate reproduction in its natural context and shaped our own work on primate mothers.

Our aim here is to present a short review of progress in our understanding of primate postnatal maternal investment patterns, with the ultimate goal of understanding the evolution of the human patterns of maternal investment. We first contrast the pattern found in small or mid-sized mammals, including most monkeys, with that among apes. There are surprising dif-

ferences. Because the typical maternal investment pattern revealed by studies of monkeys has largely shaped our view of the human pattern, finding these differences must affect our reconstruction of the ancestral human pattern. We then consider human lactation, as well as subsequent investment and care, in light of the great ape pattern.

This detailed comparative perspective allows us to identify derived features that arose during human evolution. These features, we will argue, reflect the combined effects of increased brain size and cooperative breeding. The focus throughout will be on energy intake and/or feeding time and provisioning and/or supplemental feeding. A detailed review of variation in the mechanisms regulating female reproductive physiology, such as those controlling the return to ovulatory cycles and thus conception,^{3,4} is beyond the scope of this paper.

SINGLE-SEASON VERSUS MULTI-SEASON LACTATION

Mammal species show wide variation in the way females acquire and store the energy required for reproduction. Species also vary in the degree to which females also can benefit from sea-

sonal peaks in food abundance and the degree to which they pay for reproduction from energy stores (capital breeding) or directly from food acquisition (income breeding).⁵ These two dimensions are closely linked; both depend strongly on life history. The longer the duration of infant dependence, the less females can rely on seasonal peaks because the lactation period covers both peaks and troughs in food supply. Also, the longer the duration of infant dependence, the less mothers can rely on stored body reserves because stores can only cover needs for a limited period or, for the same reason, build up an increasing deficit.

The extreme capital-breeding end of the spectrum is not found among primates, but is nonetheless instructive for our purposes. A few species store reserves before and during gestation and then quickly transfer these reserves to their infants during a brief lactation period. Mothers mostly fast during lactation, then need to recuperate to restore their condition.^{6–8} This option is only available to species in which the added weight of stored reserves does not interfere with the mother's ability to forage and escape predators. Accordingly, we mainly see this pattern among marine mammals that give birth on land or ice and have extremely short lactation periods that are fueled almost exclusively from stored reserves. Humans may show some aspects of this capital strategy because under good conditions women can build up considerable fat stores during pregnancy.^{9–11}

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Key words: weaning; cooperative breeding; life history; provisioning; food processing

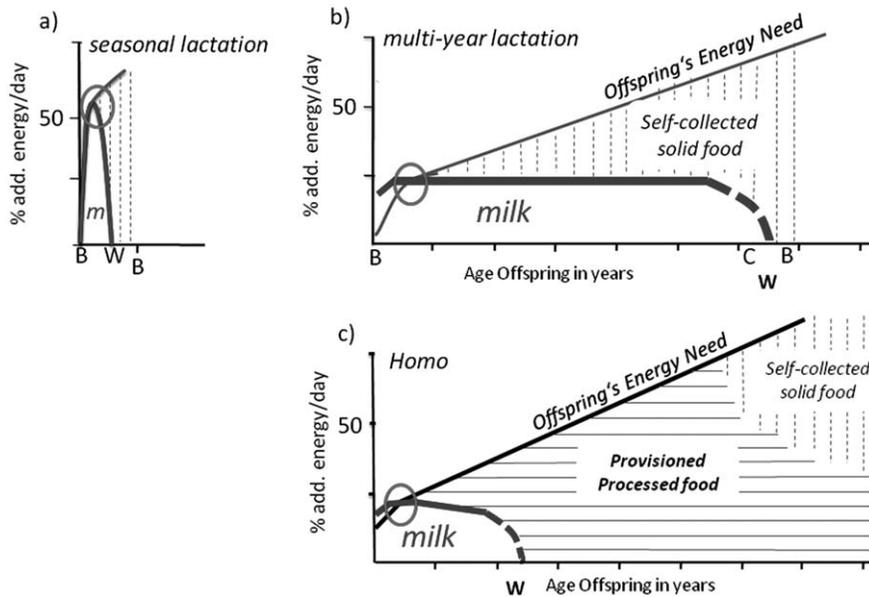


Figure 1. Contributions of mothers and offspring to the offspring's energy intake in relation to offspring age and the timing of the termination of lactation (W for weaning). A) A typical small mammal with fast lactation taking advantage of seasonal food abundance.^{40,42,86} B) A species with multi-year lactation at a stable level of maternal effort with gradually increasing infant contribution based on the 6–7 year lactation pattern in orangutans.²⁵ C) Human lactation pattern with an intermediate period of stable maternal effort. Supplements to the milk diet after a relatively short milk-only period, are provisioned and preprocessed by the mother or allomothers.^{25,74,86} After relatively early weaning, the immature is completely dependent on provisioned food for many years before it starts to contribute to its own maintenance. The red circles indicate when the mother has reached her maximum level of lactation, but milk is apparently insufficient to satisfy the needs of the offspring. Ideally, this milk insufficiency point coincides with the start of independent feeding by the offspring. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

In contrast to capital breeders, most mammal species with short reproductive cycles, especially arboreal species, tend to rely on an income breeding strategy that requires increased food intake as reproduction proceeds, with only limited storage before or during gestation.⁵ A major reason why they can do this is that most habitats show seasonal peaks in food abundance, which allow increased food intake and provide net energy gains. Most strepsirrhines and many monkeys are typical mammals in that they manage to take advantage of seasonal peaks in food abundance by timing their reproduction so that maximum lactation coincides with a predictable local food peak.¹² As a result, the classic image of the primate maternal lactation pattern is that of an inverted U, with energy transfer peaking around mid-lactation at the height of the fruiting season and corresponding to an energy intake of up to twice non-reproductive baseline levels.^{13–15} The onset of weaning comes soon after the

mother reaches her maximum lactation effort (Fig. 1A).

Not all primate taxa follow this reproductive timing, despite the fact that virtually all tropical habitats, including evergreen forests, show clear seasonality in the production of the most nutritious food items.¹⁶ Some primate species in Southeast Asia live in habitats where seasonal peaks are unpredictable due to mast fruiting, so these primates must follow an alternative tactic of seasonal breeding in which increased food abundance, rather than some 'Zeitgeber' such as rainfall or day length, is the cue to ovulatory activity.¹⁷ They thus give birth after the peak in food availability and pay for lactation through a combination of stored reserves (capital) and increased feeding (income). Taxa whose lactation periods cover more than one season, and sometimes multiple years, are also unable to rely on seasonal peaks in food abundance. Primates generally have slow life histories^{18,19} and the larger-bodied and

larger-brained monkeys, as well as all apes, have infants that develop so slowly that their periods of dependence cover multiple seasons. Thus, in species with mean birth intervals of well over one year, mothers are not able to time their period of highest need so that it coincides with any local annual food peak.

This limitation may have important implications for viable strategies of maternal investment. The long period of lactation means that females must sustain their infants through times of varying food abundance, which fluctuates on multiple time scales, from weekly changes in the quality of food patches to seasonal changes to year-to-year variation. Mothers in such species must maintain lactation across a series of peaks and troughs in food abundance. According to the data on fruiting at Tuanan, central Kalimantan (Fig. 2), for instance, some years are much better than others. This is a factor that annual breeders with single-season lactation deal with in various ways¹²: Interannual food variability may have the most impact on birth rate,²⁰ as in long-tailed macaques (*Macaca fascicularis*) or on infant survival,²¹ as in ring-tailed lemurs (*Lemur catta*). However, mothers of slowly reproducing species, such as apes, must nourish their infant during several periods of food scarcity.

At the very least, this constraint on multi-season lactators implies that mothers cannot rely solely on energy stores, as capital breeders do, simply because they would be unable to carry the large quantity of body fat required to sustain a high and stable level of reproductive effort under prolonged conditions of variable and unpredictable maternal intake. Thus, although some storage can take place during times of plenty when intake exceeds immediate needs, and some mobilization can take place during times of scarcity, it is unlikely that females can continuously incur daily deficits of energy or particular nutrients and accrue ever-increasing energetic and nutritional debts over years. Therefore, females of such species are expected to set their maximum lactation at a level that is more conservative and fairly constant, so that a steady growth rate of offspring can be achieved (as

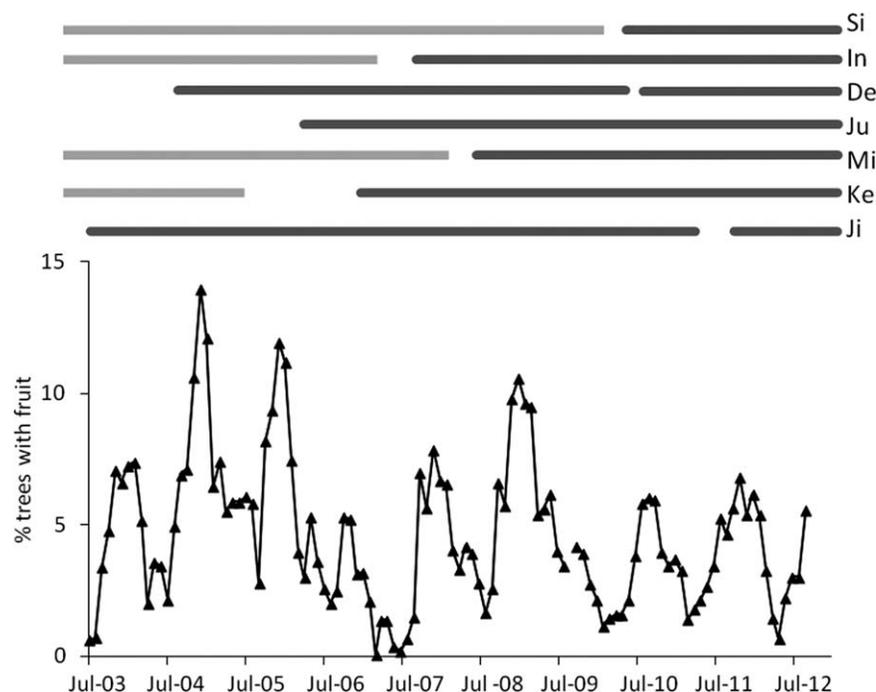


Figure 2. Monthly fluctuation in fruit availability (expressed as % of ca. 1,500 trees in phenology plot bearing fruit, July 2003–December 2012 in Tuanan, Central Kalimantan) in relation to the observed 6–7 year lactation periods of Bornean orangutans in this study area. Solid gray lines above the graph indicate lactation periods from known birth month; dashed lines indicate ongoing lactation of offspring with estimated month of birth.

suggested for humans^{22,23}) even as ecological conditions fluctuate weekly, seasonally, and across years.

This low and fairly constant level of maternal investment must, in turn, be

reconciled with the gradually increasing energy needs of the growing offspring, who faces the same problem, and is therefore also expected to favor a conservative growth rate, not

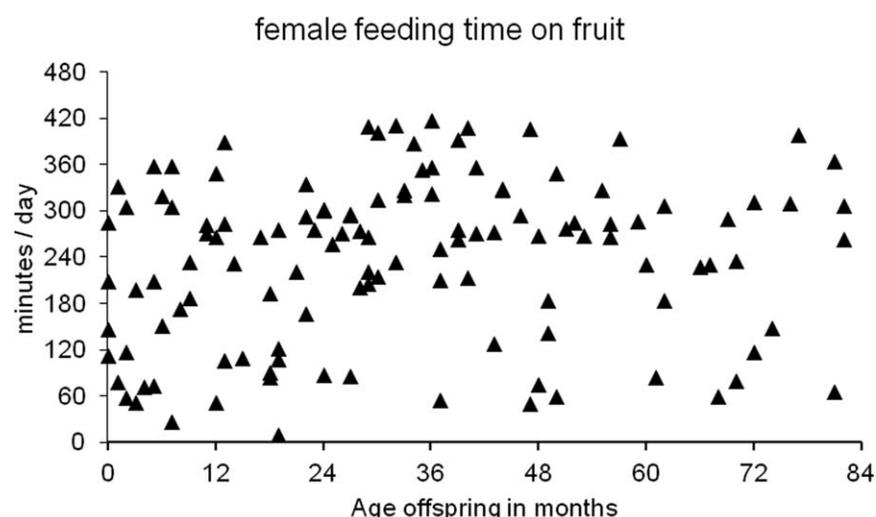


Figure 3. Maternal feeding time (in minutes per day) on fruit (on average, 70% of feeding time) of female Bornean orangutans in relation to the age of their dependent offspring. In this population, average birth interval is 7 years and in most cases weaning takes place after conception of the next offspring. Each triangle represents the average of at least 5 nest-to-nest focal follow days for a mother-offspring dyad taken within a given month. Like total feeding time, the time spent feeding on fruit does not consistently increase with offspring energy need (for more details and statistics, see van Noordwijk²⁵).

so much because growth itself is so costly, but because larger size leads to higher maintenance costs.²⁴ To compensate for a relatively low level of maternal energy transfer, ape offspring, in contrast to offspring of faster-reproducing species, should also begin self-foraging, years before they are fully weaned, to provide an increasing percentage of their own energy to augment investments by the mother. The resulting expectation, then, illustrated in Figure 1B, is rather different from that in Figure 1A.

Multi-Year Lactation

The expectation of prolonged lactation (Fig. 1B) was confirmed in a 7-year study of the activity budgets of wild Bornean orangutan (*Pongo pygmaeus wurmbii*) mother-infant dyads, covering more than 11,500 hours of observation. Orangutans may be useful as a model species because they are not just multi-season lactators, but multi-year lactators, with a 6–7 year lactation period in this population.²⁵

We found that after an initial rise in feeding during the first half year of offspring life, the age of the dependent infant had no effect on a mother's feeding or travel time.²⁵ Thus, overall, maternal feeding time was remarkably stable throughout each infant's dependent period, although it obviously depended on the fluctuating food availability, so that mothers spent less time feeding when fruits were more abundant. Figure 3 shows the intake of fruit as a function of infant age and the clear lack of influence of infant age, despite a significant and strong effect of fruit abundance (data taken from van Noordwijk and colleagues²⁵). Estimates of actual food intake based on the caloric value of females' monthly diets in the same population²⁶ suggest that intake is higher during periods of fruit abundance, but also that infant age does not significantly affect a mother's intake after a gradual increase during the infant's first year (ER Vogel, personal communication). This constant effort is very different from the feeding time or food intake estimates

reported for small, seasonally breeding primates, which show a characteristic peak around the middle of lactation.^{14,27,28}

For other apes, only a few studies report maternal feeding effort or food intake across the period of lactation. However, the data that are available suggest that other apes may follow a similar pattern. In chimpanzees (*Pan troglodytes*), there was no effect of infant age on maternal feeding time at Mahale.²⁹ Also, a study from Gombe³⁰ presents a comparison of lactating females lumped over all seasons and infant ages, with smaller samples of pregnant and non-pregnant-nonlactating females, suggesting that infant age does not obviously explain variation in females' time budgets. Similarly data from Kibale⁴ suggest that mothers fluctuate around a rather stable energy balance throughout their 3–4.5 year lactation period. A study of siamangs (*Symphalangus syndactylus*) showed inconsistent differences in maternal feeding time during the early, peak, late, and postlactation phases for 5 females, suggesting, at best, a minor effect of infant age.³¹ Thus, available data, although patchy, suggest that the orangutan pattern of prolonged stable maternal effort may hold for other apes as well. Indeed, even species that have shorter birth intervals but are multi-season lactators and thus are intermediate between apes and seasonal species, show a more constant maternal effort than expected. For instance, in baboons, which have interbirth intervals of approximately 1.5 year, females increase feeding time in the few months after giving birth but subsequently reach a sustained plateau.^{1,32}

A second finding of the orangutan study was that maternal feeding time, and thus average mean intake, was estimated to be only about 20%–25% higher than that for an adult female without dependent offspring.²⁵ Values on baboons vary between 0%–57%, depending on methods and habitat or living conditions.^{32–35} These increases are quite modest compared not only to those of the typical female small mammal, which can increase their intake 2–4

times during the (short) period of maximum lactation,¹³ but also compared to small primates, including brown lemurs (*Eulemur fulvus*), which can increase their uptake 2–3 times,¹⁴ and marmosets (*Callithrix jacchus*), which, with twins, can increase theirs by almost twice.¹⁵

The third notable finding was that early in their second year orangutan infants began substantially to supplement their milk intake with solid food that they harvested themselves. But unlike the situation among most other mammals and small primates, there was no subsequent reduction in maternal feeding effort, suggesting that offspring milk intake probably remained constant as self-

Our analyses suggest that orangutan infants are weaned, as shown by a decrease in suckling attempts outside of the nest and a strong reduction in nest-sharing during the night, only when they have been providing more than half of their energy needs for some time.

provisioning increased. Thus, during a period of about 5 years after the initiation of independent feeding, the infants appeared to sustain their gradually increasing needs by supplementing a relatively constant level of milk intake with more and more self-provisioned solid food. Our analyses suggest that orangutan infants are weaned, as shown by a decrease in suckling attempts outside of the nest and a strong reduction in nest-sharing during the night, only when they have been providing more than half of their energy needs for some time.²⁵

Unfortunately, our sample size was too small to evaluate how mothers' energy budgets responded during the last year of lactation and wean-

ing. Moreover, we could only measure feeding effort, not lactation effort. However, because orangutans typically have conceived before completely weaning their prior offspring, reproductive effort at the time of weaning has probably already partly shifted from lactation to preparation for the next reproductive cycle, perhaps involving recovery of maternal body condition and modest fat deposition.

Both chimpanzees and gorillas (*Gorilla gorilla*) also show a gradual increase in infants' own foraging effort from 6–12 months of age onward.^{36–38} This, coupled with lack of evidence of peaks in maternal effort, is consistent with the pattern we have documented in orangutans. Baboons, with a lactation period of about one year, also show a similar pattern. Altmann¹ and Barrett, Halliday, and Henzi³² showed that infant baboons start to supplement milk with independent feeding on solid food at around 4–6 months of age, but their mother's feeding time remains stable for several more months.

Figure 1B summarizes the three distinctive characteristics of maternal effort in species with slow infant development that extends over multiple seasons: maternal effort remains roughly constant over long periods, sometimes even years; maternal effort is only moderately increased relative to baseline levels; and maternal effort is not responsive to the onset and increase in an infant's own food intake. These differences may have implications for the dynamics of mother-offspring conflict (Box 1) and how we conceptualize weaning.

The Meanings of Weaning

Weaning is a notoriously ambiguous term. It can refer to the process of decrease and cessation of milk provisioning by the mother or the switch from a milk diet to a more 'adult' diet by the immature. The transition from an infant's full dependence on milk to its complete reliance on adult food can take place over a few days, as in mice (*Mus domesticus*³⁹), but may last longer

Box 1. Mother-Infant Conflict

Mother-offspring conflict, as Trivers formulated it,⁵¹ can pertain to both the rate of maternal investment and the timing of cessation of investment (classic weaning conflict). The paucity of reported behavioral conflict about the rate of investment among primates may reflect the fact that during the early post-natal period, unlike the prenatal period,⁵² the mother is in control and infant growth trajectories are conservative to avoid starvation. The avoidance of starvation is especially important in larger-brained species.⁵³ This means that most of the time the interests of mother and infant about rate of investment largely coincide.

Most work therefore concerns termination-conflicts. These conflicts need not be limited to the mother's being a source of milk. Especially among primates, they are also about the mother being the provider of transportation. Several primate studies have reported 'carrying conflicts'.^{1,54-56} Such conflicts should be unique to primates and a few other species that carry their young and are expected to precede the conflict over milk because foraging independence cannot be achieved without locomotor independence.

Termination-conflict should be most severe when termination is abrupt. Termination of lactation is expected to be forced in seasonal annual breeders. Females conceiving too late may have to skip an entire year, which may comprise a substantial portion of the adult reproductive career. Indeed, behavioral conflict around weaning is reported for such species.^{14,57-59} On the other hand, the delay of weaning for a short period is less costly among non-seasonal breeders and species with multi-year lactation, for which the conflict would be about a modest postponement of the next conception.

Indeed, the weaning conflict is reported to be rather mild in several of those taxa,^{55,56,60} although quantitative comparisons are lacking.

Natural selection should ensure that the age at which the infant begins to harvest solid food on its own roughly coincides with the moment the constant supply of mother's milk is just beginning to be insufficient to cover the infant's energetic needs (Fig 1B). In this way, the gradual increase in the infant's feeding effort keeps pace with its growing needs due to larger body size. However, by the time of the "milk insufficiency point."²⁵ when the mother's lactation level no longer fully meets its needs, the infant, especially if it is not yet able to increase its feeding effort, may try to coax more milk from the mother than is optimal for her to give. This conflict, then, should occur relatively early in the lactation period, which in apes is around one year of age. It should be especially pronounced when the mother's level of maximum lactation is relatively low as a consequence of prolonged food shortage, but the infant is not yet capable of providing its own food, in part because of the poor conditions.

To our knowledge, no detailed studies have examined the time course of mother-infant conflict in apes, but we predict that they will also experience conflict around the age of the mother's *maximum* lactation and the time when infant needs overtake maternal output. This model leads to a testable prediction: We expect that the age when offspring requirements exceed maternal supply, which varies across species, will be marked not only by behavioral conflicts, but by a reduction in offspring growth rate as the infant must begin to harvest its own food (Fig. 1B).

Consistent with these expectations, naturalistic observations of slowly reproducing species have documented evidence of infant distress that is not related to classic weaning conflict. In baboons, an increase in maternal rejections of infants' suckling attempts coincided with the onset of independent feeding, which occurred at several months into lactation, around the time that mothers reached their maximum sustained feeding effort^{32,61} and almost half a year before the termination of lactation.

A similar increase in mother-offspring conflict was found in elephants around the time calves started to feed independently, which was years before the end of lactation.⁴⁷ Thus, at least in some species with long lactation, the onset of independent feeding has been found to coincide with a little-recognized increase in mother-offspring conflict at a different time from the classic weaning conflict, in that it occurs relatively early in lactation and long before the final reduction in maternal resource transfer. Careful documentation of such conflicts can distinguish them from behavioral conflicts between mothers and infants that might result from coordination or scheduling problems: An infant needs to learn not to interfere with its mother's activities.^{1,42}

The complexity of the issues surrounding mother-infant conflict, including the conditions in which it is behaviorally expressed, suggests that as a community we may have somewhat neglected this topic because of the existence of an elegant model, which suggested that the case was closed. However, the time may be ripe for additional studies of the sort pioneered for baboons to examine the rates and contexts of mother-infant behavioral conflict and their timing relative to weaning and other developmental landmarks.¹

than the milk-only phase of lactation, as in many larger mammals.⁴⁰ Still, in most species, the onset of infants' feeding on nonmilk food also marks the onset of the reduction in maternal investment^{41–43} because the mother responds to this sign of the offspring's digestive maturation with a progressive decline in milk transfer.⁴⁰

This pattern has led to the widespread assumption^{40,42–45} that there is a causal relationship between the infant starting to feed independently and the mother starting to reduce her milk transfer.^{42,44,45} This may well characterize both the pattern and the causal structure in smaller mammals, but it does not characterize the pattern seen in more slowly developing species. A pattern similar to that in the orangutan is found in humans^{23,46} and in other large mammals with multi-year lactation, such as elephants (*Loxodonta africana*)^{47,48} and giraffes (*Giraffa camelopardalis*).⁴⁹ This demonstrates that the onset of infants' independent feeding is not inevitably accompanied by a decrease in the mother's investment in milk. Instead, the infant's solid food intake increasingly supplements a continuous and stable level of milk intake. Thus, rather than simply assuming that weaning automatically begins when infants begin to feed independently, we should recognize the separate trajectories of maternal investment and infant feeding activity and refer to 'weaning' only when maternal investments are actually declining.

Similar confusion surrounds the term 'weaning foods,' which refer to foods eaten by infants during the transition from dependence on milk to full nutritional independence.¹ These foods are thought to be easily harvested and highly digestible. Indeed, it has been suggested that the peak availability of such foods, such as flowers, was the selective advantage for the timing of seasonal reproduction in baboons.¹ In species with short lactation, this notion is meaningful, but in species in which infants augment milk intake with solid foods over multiple seasons or even years, it obviously is not.

We expect selective intake of highly digestible food items to occur

around the age when an infant begins to eat solid foods in addition to milk, rather than around weaning, which is years later. However, in orangutans, we find no particular order in which infants start to eat flowers, insects, fruits, leaves, or bark (MA van Noordwijk, unpublished). Instead, infants appear to eat whatever they can process when they start to eat and largely copy their mothers' food selection.⁵⁰ We know of no study among species with multi-year lactation that has evaluated in detail whether the foods infants consume during their first months of supplemental independent feeding show special characteristics. If they do, this could indicate that mothers with infants of a particular age target food sources so that their infants also consume these 'weaning' foods.

HUMAN MATERNAL INVESTMENT PATTERNS: ANCESTRAL AND DERIVED ELEMENTS

Reconstructions^{40,44} of the ancestral state of the human maternal investment pattern have often implicitly relied on the seasonal primate pattern of Fig. 1A. If additional data from other species continue to support our interpretation of the orangutan data, it will be more realistic to use the multi-year lactation pattern depicted in Fig. 1B to characterize the ancestral state of the human lineage. It is therefore interesting to see what we can learn about the derived features in humans, specifically the changes that took place after the hominin lineage split off from the last common ancestor with the two *Pan* species.

These changes must be viewed against the backdrop of major life-history differences between humans and other apes.^{62,63} First, humans reach the age of first reproduction much later and live longer than other apes do. Larger-brained species are generally forced to allocate less energy to growth and reproduction,⁶⁴ but compensate for their slower development and lower birth rates with a longer lifespan, which probably is why selection favored

larger brains.^{64,65} Much of the ape-human difference in age at first reproduction and total lifespan may therefore be attributed to our much larger adult brain size. Second, and in contrast to the general trends in mammalian life histories,¹⁹ human women show high birth rates.⁶⁶ Human babies are fully weaned much earlier than are those of other great apes, at ca. 2.5 years among foragers^{67,68} rather than the 3–8 years among other great apes.⁶⁹ A third difference is that human mothers sometimes must simultaneously provide care for multiple immature offspring, who are fully weaned from milk but still unable to sustain themselves.²⁴ Also, human mothers enter menopause well before somatic senescence,^{66,70,71} while in apes reproductive and somatic senescence occur in parallel.^{72,73} Figure 4 provides a summary of the differences that concern maternal investment and infant development.

Ancestral Features of Maternal Investment

We predict that humans will exhibit several of the same features of maternal investment that we have documented in orangutans: a long, multi-year lactation at a moderate level, accompanied by an early start of nonmilk food intake by the infant, which leads to a long period during which the mother's fairly constant contribution covers a gradually reducing portion of the infant's needs. Very much like orangutan mothers, human mothers that nurse their babies show multi-year lactation with a relatively stable maternal energetic effort.^{46,74} Although detailed data are lacking, it is reasonable to assume that the lactation effort of human foragers is similar to that reported in these studies.^{46,74} Thus, lactation increases toward a maximum around 6 months postpartum, when supplemental provisioning starts. Importantly, even with supplemental feeding, milk output stays at a rather constant level over the next 2 years, albeit probably slightly lower than the maximum,⁴⁶ while milk quality, which is very similar to that of other apes,⁷⁵ also

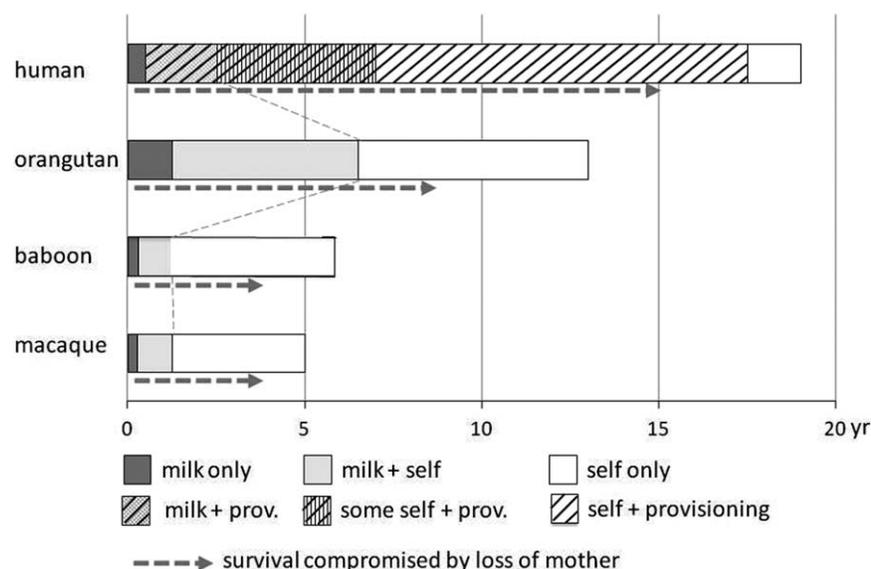


Figure 4. Duration of different periods of maternal investment and care and offspring development until female age at first birth in representative cercopithecine monkeys (long-tailed macaques, *Macaca fascicularis*^{20,56}; savanna baboon, *Papio cynocephalus*^{1,32,103}), a great ape (Bornean orangutan, *Pongo pygmaeus wurmbii*²⁵), and human foragers.^{70,82} Arrows underneath the bars indicate until what age the presence of the mother has been shown to affect an offspring's fitness through a direct effect on survival or adult success, mediated by factors such as dominance rank. In all these primates, extensive post-weaning maternal care affecting the offsprings' reproductive success has been demonstrated. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

seems to vary little over this period.²³

At birth, human infants are relatively heavy, large-brained, and fast-growing. Nonetheless, women have a maximum lactation effort set at a modest level of daily energy transfer.²³ Human lactation requires an increase in food intake of only ca. 15%-30%, varying among individuals and populations,^{46,76} partly due to mothers' differences in activity level and chronic nutritional status.⁷⁶ This human value is similar to the maximum estimate of ca. 25% in wild Bornean orangutans,²⁵ but far lower than estimates for small seasonally breeding mammals.¹³ (Unfortunately, estimates for seasonal primates are scarce.) Levels of milk transfer are similar in humans and orangutans, but human babies are larger and their energy needs increase faster, so they reach the point at which milk no longer supplies all of their needs at a younger age than do other ape infants.

Thus, the long overlap between continued nursing and consumption of solid food by human infants is probably an ancestral pattern that

predates the divergence of the human lineage. Even though the details are different, the milk diet of human infants, at least among foragers, is supplemented by nonmilk food after a relatively short milk-only phase of lactation. Just as in other great apes, this milk-plus-solid-food phase lasts for a long time before weaning starts (in the sense of a steep reduction in milk transfer).

Uniquely Human Features

The basic similarities in lactation pattern help to illuminate the unique, derived features of the human maternal investment strategy. First, human babies are much heavier and fatter at birth than are other great apes.⁷⁷ Second, human milk is supplemented with additional food⁶³ beginning at a somewhat earlier time than the age of self-provisioning in other great apes. Third, and more importantly, these first solid foods are not self-collected foods, but specially prepared complementary foods provided by the mother and allomothers (all caretakers other than the mother). Fourth, the total duration of human

lactation is much shorter, and human babies are fully weaned much earlier than are other apes, despite having bigger brains and, accordingly, higher energy needs. Finally, human offspring, unlike offspring of other apes, continue to rely on foods provided by others for many years after complete weaning. Humans do not typically achieve nutritional independence until they are about 18 years old⁷⁰ and maximum foraging efficiency may be reached even later.⁷⁸ This combination of high offspring needs and low maternal investment points to the central role of energy inputs from alloparents in the human reproductive strategy.⁷⁹

Human newborns are unusually fat at birth⁷⁷ and their early rapid weight gain after birth largely reflects additional extensive fat deposition.^{74,77,80} Thus, during the first months after birth, the mother's milk supply is partially used for infants' storage reserves, which buffer future fluctuations in energy input. Such extensive infant fat storage is not seen in other great apes. Although it also occurs in species with long or complete absence of the mother, such as seals, which have a very short lactation period,^{6,8} human infants' postnatal adiposity is unlikely to be a response to long maternal absences. Instead, it is a derived adaptation to reduce the risk of malnutrition in the absolutely and relatively large infant brain, which, at this age, is responsible for more than half of the energy expenditure.⁷⁷ Because brain metabolism is inflexible, the human infant is especially sensitive to energy deficits.⁷⁷ Although rapid early brain growth, taking advantage of the mother's early lactational overcapacity, is also found in chimpanzees⁸¹ and suspected in orangutans, it is set at a much higher level in humans.⁸²⁻⁸⁴ The solution of supplying the infant with internal reserves to buffer fluctuations in natural food supply is not feasible without concurrent changes in patterns of infant carrying.⁸⁵

Around the end of the first half-year, the human infant is twice as heavy as at birth and reaches a point when milk output only just matches

the infant's needs.^{77,86} (This point is probably reached a few months later in apes⁸⁷ and, at least in wild populations of chimpanzees³⁶ and orangutans,²⁵ infants start to feed on some solid food when they are 6–12 months old). At this point, the human infant already needs complementary foods to avoid having to mobilize its own stored reserves and experience growth faltering. Whereas the start of the intake of solid food varies across cultures, the human infant receives non-milk food from its mother and other caregivers, whereas ape infants have to acquire this themselves. Although food sharing from mouth to mouth is occasionally seen in orangutans and chimpanzees, it is almost always preceded by the infant's begging, and seems to function more as transfer of information than calories.⁸⁸ In humans, the provisioning is proactive, reflecting the initiative of the caregivers. A second major difference is that this early food is also actively processed by premastication⁸⁹ or other forms of pre-processing, such as mashing, cutting, or cooking.⁹⁰

Once supplemental feeding is established, a human mother sustains investment in milk at a constant level for about 2 years, albeit in most populations at a somewhat reduced level compared to maximum output during early lactation.^{46,91} The early caloric subsidies of provisioned, easily digested food explain how human infants in non-industrial societies can be weaned at around 2.5 years, on average,⁶⁸ much earlier than infant chimpanzees, orangutans, and even gorillas, and despite the equally modest rate of maternal energetic investment by human mothers.

While other great ape mothers are tolerant of their infant taking food from them, they tend to be much less tolerant toward their weaned offspring.^{60,92} Among humans, in contrast, relatively early weaning is followed by continued provisioning of immatures over many years. During the first few years after weaning, this provisioning, which typically accounts for most of immatures' food intake, gradually decreases to a variable

degree,⁹³ but continues even up to adulthood.^{70,86}

Cooperative Breeding and the Human Pattern

A reconstruction of the selective processes that led to this derived pattern of reproductive investment in extant humans may never be fully verified. However, there are good reasons to believe that allomaternal care has been an important facilitator of the evolution of this suite of derived traits. Hrdy, in particular, has stressed that humans are cooperative breeders.^{79,94} Human fathers participate in raising offspring by provisioning both food and care,⁹⁵ as do other adults,⁹⁶ including, to a

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variable extent, post-menopausal women or, in other words, grandmothers.⁷¹ These inputs of energy and time allow women to wean early despite modest maternal investment in milk. Although obligate cooperative breeding is rare among primates, found only in the callitrichid monkeys of the Neotropics, allomaternal care is more common. Across species, more allomaternal care means shorter birth intervals, and thus earlier weaning.^{97–99} Much allomilk care is in the form of infant carrying, but among callitrichids there is also

provisioning.⁹² In humans, allomaternal care is more intense and systematic than in any other primate, and the impact on weaning age and interbirth interval is accordingly much stronger.

Humans are unique in that provisioning of prepared foods supplies a large proportion of the infant's energy needs. Much of the food that is provisioned is preprocessed through cutting, mashing, and cooking. Some, but by no means all of this food is meat obtained through hunting, and perhaps among earlier hominins, by scavenging. These inputs allow human mothers to restrict their maximum level of lactation so that the infant reaches the milk insufficiency point (MIP) at around 6 months,⁷⁴ the age at which the infant typically begins to ingest non-milk food.⁶⁸ Both of these points are somewhat earlier in humans than in apes, suggesting a process of coevolution between allomaternal care and the trajectory of infant growth and development. Dental maturation probably started to slow down around *Homo erectus* relative to the great ape and australopithecine pattern,¹⁰⁰ even though milk yield became insufficient to fully sustain the infant's needs. This suggests that early supplementation through premasticated foods began around that time in the hominin lineage, and may have gradually become earlier as technology improved.

The reduction in weaning age in humans is even greater than the reduction in the age at which non-milk food is added.^{64,65} We suggest that this reduction required an improvement of caloric yields in foraging by caretakers, which in turn probably required improvement of technology and foraging skill. We thus predict that over the course of human evolution, the age of weaning has gradually declined. This also suggests that our demographic viability, as expressed in potential population growth rates, gradually increased in parallel.

As our hominin ancestors pushed the weaning age back by several years, they created a class of juveniles (weaned immatures) that lacked appropriate locomotor and foraging

skills and abilities (including both selection and processing). Although they provided some food for themselves, these juveniles remained dependent on adults for a substantial period. The uniquely human life-history stage of childhood⁶⁶ is simply the period during which the immatures of other ape species are still infants, supported partly by mother's milk and partly by independent foraging, and partly dependent on others for transportation.

The human pattern of weaning before locomotor independence is reached would be impossible in other primates. Indeed, bipedal human weanlings are still very inefficient in their locomotion. They cannot keep up with foraging adults for several years after weaning, and must be carried.⁸⁵ This greatly reduces their mothers' foraging efficiency. Among extant foragers, immatures who are weaned but too small to keep up with a group of gathering women can stay in camp during the day.¹⁰¹ Thus, central places must historically have been present before the time when weaning age became earlier than locomotor independence. This could have been rather early in the evolution of the genus *Homo*, given that human children reach adult-level time away from camp around the age 6 or 7 years.¹⁰¹

One more correlate of intensive cooperative breeding is also found in hominins. Mammalian lineages with cooperative breeding, especially if this includes provisioning, tend to have larger brains than do lineages of independent breeders.¹⁰² Again, large brains tend to slow the pace of development. The reliable external input of more energy through provisioning lifts this developmental constraint, allowing brain size to increase over evolutionary time.⁶⁴

CONCLUSION

Like other great apes, humans have a lengthy period of lactation sustained over multiple good and bad seasons with a level of energy intake that is only slightly elevated above the non-reproductive baseline, suggesting that these may be ancestral

ape features from which the human pattern was derived. Despite these similarities, human infants reach the point where milk cannot cover all their needs at an earlier age than do other apes (compare Fig. 1C with Fig. 1B). In contrast to the other apes, in humans this point is not the time when infants start to gather or process their own food, but rather when provisioning with pre-processed food begins. The combination of a cooperative breeding system and advanced techniques for processing highly nutritious food enabled efficient and active provisioning to immatures by mothers and others. The period of provisioning became ever more prolonged, ending up covering most of immaturity. Thus, during hominin evolution, the advent of provisioning of young dependents, unweaned as well as weaned, modified the ancestral ape strategy of prolonged multi-year lactation, making possible the evolution of larger brains despite modest maternal investment in lactation. Collectively, these innovations permitted the evolution of a suite of life-history characteristics, that help define modern humans, including earlier weaning, reduced birth interval, and higher fertility rates.

ACKNOWLEDGMENTS

We have been inspired by both Jeanne Altmann and Sarah Hrdy to study mother-offspring interactions in the wider ecological and social context. We thank Judith Burkart, Karin Isler, and Erin Vogel for discussion; we thank Joan Silk, Phyllis Lee, and anonymous reviewers for feedback and comments on the manuscript. We acknowledge the financial support of the A.H. Schultz Foundation and SNF.

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