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ENERGY COSTS OF LACTATION

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INTRODUCTION

The diversity of mammalian species attests to the success of lactation as an evolutionary strategy. Although the length of lactation relative to gestation varies considerably between altricial and precocial mammals, the newborn from all species require milk in the early stages of development. The benefits of this adaptation must therefore outweigh the costs. However, the costs to a mother can be high. In most mammals the stress of lactation induces a larger change in the energy budget than occurs at any other time of life, and total caloric flux may increase by two- to three-fold (30).

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HUMAN LACTATION IN A ZOOLOGICAL PERSPECTIVE

Primates in general, and humans in particular, are characterized by very slow rates of postnatal growth, and this is reflected in both the composition and volume of their milk. Allometric analysis of all available data from mammalian species demonstrates a roughly parallel relationship between milk energy yield at peak lactation and maternal metabolic body size. Oftedal (25) demonstrated that within this overall relationship there are at least three grades representing special adaptations: species with many young, ungulates with single young, and primates. This division yields very high correlation coefficients between maternal size and milk output within each group and demonstrates that primates represent a distinct group with much lower milk outputs than other species. Table 1 lists estimates of peak milk energy output as a function of maternal body weight$^{0.75}$ and demonstrates that in primates the requirements for milk production are between 4- and 15-fold lower than in the other species listed. It is the very low stress of human lactation per unit time that determines the mother's immediate physiological responses (30). An obvious illustration of this is that a woman only needs to increase her food intake by about 25% to meet the full costs of lactation, whereas a rat with eight or more pups must increase her intake by 300% or more. In the rat this necessitates marked anatomical changes including hypertrophy of the digestive organs, liver, and kidneys in order to handle the increased nutrient flux, but there are no reports of such changes in women.

The calculations in Table 1 are of the stress per unit time and may exaggerate the differences between primates and other species in terms of the total costs of lactation since these depend on its duration. Unfortunately, attempts to calculate the total costs of "normal" lactation in humans are somewhat meaningless since the natural duration of lactation is not known. However, breast-feeding in developing countries commonly continues for 2–3 times the length of gestation. This is considerably longer than in most other animals, and as a consequence the overall costs of lactation may be rather similar to many species with higher milk output.

Another characteristic of human reproduction is the very large subcutaneous fat deposits available to subsidize the additional costs when dietary intake is restricted (30). The marked sexual dimorphism in humans provides the average female with twice as much stored energy as the male, and in this respect humans differ from most other primates. This combination of low requirements per unit time and extensive energy reserves provides women with a unique capacity to meet the additional costs of reproduction by a variety of short-term adaptive strategies.

Table 1 Peak milk energy yield relative to maternal metabolic body size[a]

	Daily milk energy/body weight$^{0.75}$ (kJ/kg)[b]
Laboratory animals	
Mouse	1350
Rat	1000
Rabbit	750
Guinea pig	350
Domesticated animals	
Cow	
Dairy	1400
Beef	250
Goat	
Dairy	1150
Bedouin	450
Pig	1000
Sheep	500
Primates	
Baboon	100
Human	100

[a] Data compiled from Refs. 25 and 30.
[b] 4.184 kJ = 1 kcal.

CURRENT PRINCIPLES USED TO CALCULATE ENERGY COSTS

The 1985 FAO/WHO/UNU expert committee on energy requirements calculated the costs of lactation simply by adding the computed costs of milk synthesis to the requirements of a nonpregnant, nonlactating woman (10). The resultant recommendations are for an increment of about 2090 kJ/day throughout lactation. This assumes that the extra fat deposited during pregnancy is mobilized during the first six months of lactation to provide 835 kJ/day. If this does not occur, the increment during this time should be 2930 kJ/day.

The incremental costs of milk synthesis are calculated as the sum of the energy content of the milk plus the energy required to produce it. The 1985 report used median milk intake values collected in a WHO multicenter collaborative study of Swedish women (39) and assumed an average energy content of 290 kJ/100 g. The efficiency of converting dietary to milk energy was assumed to be 80%, on the basis of a study by Thomson, Hytten & Billewicz (36). This estimate was derived by a very indirect calorimetric balance procedure in which the difference in energy intake between groups of lactating and nonlactating women was taken to be the energy used for milk synthesis. The energy content of the milk was not measured but was estimated from the infants' growth rates. From these figures the estimated efficiency of milk synthesis was 97% and the value of 80% was taken as the lower 95% confidence limit (10). In view of the method of derivation and the fact that the estimate is higher than in other species, the value of 80% efficiency requires reappraisal.

The calculations of energy requirements published by FAO/WHO/UNU (10) and by national committees are inevitably rather crude since they are only intended to provide approximate guidelines for an average woman. Apart from the efficiency figure for milk synthesis they contain a number of other assumptions that may not be entirely justified. These are reexamined in this review.

CALCULATION OF THE NET COSTS OF MILK PRODUCTION

Energy Transfer to Milk

For the purposes of calculating the total costs of lactation, we use reasonable average figures for the volume and energy density of milk from adequately nourished women, recognizing that there are wide within- and between-subject variations in both. In the context of this review, errors in the estimate of milk energy have a relatively trivial impact since the energy transferred as milk on average represents only 20% of the mother's intake.

A recent comprehensive review of milk intakes in fully breast-fed infants at three months of age concluded that the average value was close to 750 g/day in women from both affluent and developing nations (29). With the exception of two studies that reported unusually high intakes, the range of group means was 620–840 g/day in affluent countries (13 studies) and 630–820 g/day in developing countries (9 studies). Most of the estimates reviewed were made by test-weighing and none made corrections for the infant's insensible water losses during the periods of suckling; this may have led to an underestimate of 3–5%. Allowing for this, the value of 750 g/day is consistent with the estimates obtained by the WHO multicenter study, although the intakes eventually used by the FAO/WHO/UNU committee were increased by 6% to allow for a perceived underestimation (10, 39).

The energy content of breast milk has usually been calculated by applying the modified Attwater factors to chemical estimates of the proximate constituents and therefore represents metabolizable energy. Protein and nonprotein nitrogenous substances contribute only about 8% of the energy in mature milk, and errors in the estimate are therefore of little consequence. We assume here a protein content of 1.2 g/100 ml. Lactose is the least variable component of human milk, and when correctly assayed shows a concentration of close to 7.0 g/100 ml; group means from a large number of studies of affluent women fall between 6.8 and 7.4 g/100 ml. There is some evidence that milk from women in the developing world may have a slightly higher lactose content at about 7.5 g/100 ml. Milk fat is the most variable and energy-dense component, and creates the most difficulty in devising satisfactory sampling protocols. All protocols so far devised are open to some criticism and none can claim to give a perfect assessment of the amount of fat transferred to the infant. However, in spite of these problems, it seems probable that the fat content averaged over the whole day in well-nourished women is close to 4.0 g/100 ml. Studies with reasonable sampling protocols give group mean values ranging from 3.6 to 4.6 g/100 ml. Although there have been many claims that milk fat is lower in women from the developing world, this conclusion does not stand up to a critical review of the methods used. Most modern studies have failed to demonstrate differences between countries and especially between well-nourished and poorly nourished women from the same country when studied using the same experimental protocol. Lack of space precludes citation of the many studies reviewed to derive these compositional figures. Several reviews are available (11, 16, 23).

Using these estimates of milk composition gives a computed metabolizable energy content of 285 kJ/100 ml and a gross energy of 300 kJ/100 ml. Measured by bomb calorimetry, the gross energy content of milk is about 310 kJ/100 ml (14). A recent study has attempted to assess the energy content of breast milk indirectly by measuring energy expenditure and the composition of new tissue formed during growth (20). The advantage of this approach is that it represents milk energy as metabolized by the baby, but it has several disadvantages, including the number of assumptions necessary in the overall calculation. The calculated metabolizable energy was 240–250 kJ/100 ml in early lactation. With the exception of this last study, the overall variation in group mean values for either metabolizable or gross energy therefore span a range of only about 10%, which will have little effect on the calculation of the average energy costs of lactation.

It must be stressed that this consistency only refers to group means. There is a considerable between-subject variability within any group studied. For milk volume the coefficient of variation for estimates made by test-weighing over four continuous days (and hence minimizing the component of within-subject variability) is approximately 23% (29). The between-subject coefficient of variation for lactose is about 7% and for fat is about 25%. Combination of all of these components of variability yields an estimated between-subject coefficient of variation for energy transfer in milk of about 30%, which indicates an expected four-fold range.

Energy Cost of Milk Synthesis

BIOCHEMICAL EFFICIENCY In principle it should be possible to compute the biochemical efficiency of synthesizing each of the proximate constituents of breast milk from the known stoichiometric equations and the obligatory heat losses associated with each step of the synthetic process.

Protein synthesis is the simplest and energetically least important of the processes to consider. Blaxter (3) assumed that three ATPs are required to synthesize each peptide bond and that the average molecular weight of amino acids in a representative milk protein is 100. Thus three moles of ATP, each with an energy content of approximately 80 kJ per pyrophosphate bond, would be required to synthesize 100 g of protein. Using the example of casein, with a heat of combustion of 2440 kJ/100 g, one can compute the efficiency of synthesis as $2440/(2440 + 240) = 91\%$. Current estimates assume at least four ATPs per peptide bond and the recalculated efficiency is 88%. This value does not differ appreciably for other proteins but is likely to represent the maximum possible efficiency for several reasons.

Firstly, it makes no allowance for any transport costs of the amino acids from plasma to the endoplasmic reticulum, nor of the proteins through the Golgi system and into milk by exocytosis. The calculation also assumes that the amino acid mixture in the plasma pool is perfectly matched to the composition of the milk proteins and that no specific synthesis of amino acids is required.

Lactose synthesis from glucose requires a total of three moles of ATP per mole of lactose formed. The efficiency of synthesis calculated as the heat of combustion of the end products (5650 kJ/mole) divided by the heat of combustion of glucose (2×2820 kJ/mole) plus the energy equivalence of the three pyrophosphate bonds (3×80 kJ/mole) is 96%. Since blood glucose must be derived from liver glycogen for most of the day, it is also necessary to consider the waste heat associated with glycogenolysis. The efficiency of glycogenolysis is computed to be 98.7% (7), which gives an overall efficiency for the glycogen-glucose-lactose process of 95%. This is clearly an efficient process, but as with the protein synthesis these calculations only include the basic biochemical costs of the chemical reactions involved and must therefore represent an absolute maximum.

Triglyceride synthesis is much more complex and necessarily involves a number of approximations. These primarily involve assumptions concerning the differing chain lengths of the fatty acids, the metabolic pathways used to provide the reduced NADPH for fatty acid synthesis, and the proportion of fatty acids that are incorporated into milk by direct transfer from the blood stream rather than by de novo synthesis in the breast.

Fatty acids with chain lengths up to C14 (myristic acid) are assumed to be synthesized in the breast with C14 itself predominating (23). Under conditions of low dietary fat intake, longer chain fatty acids will also be synthesized de novo (6, 23). Elia & Livesey (7) calculated the efficiency of synthesizing dioleyolpalmityltriglyceride from starch according to whether the pentose phosphate cycle or the malate cycle predominates in the provision of NADPH. [The activity of NADP isocitrate dehydrogenase is reported to be low except when acetate is an important precursor for fatty acid synthesis (5).] Under conditions of maximum pentose phosphate cycling, the conversion of 17.2 moles of hexose equivalents into 1 mole of triglyceride dissipates 14,860 kJ and the efficiency emerges as 69.5%. Under conditions of maximum malate cycling, the conversion of 15 moles of hexose equivalents dissipates 8720 kJ to give an efficiency of 79.5% (7). In the rat, the pentose phosphate pathway accounts for at least half of the NADPH production (18) and it seems reasonable to use this assumption for human synthesis. The overall efficiency would therefore be 74–75%. This matches Flatt's calculation of 74% efficiency for the synthesis of palmitic acid from starch since the additional costs of esterification are very low (12). The efficiencies for fatty acids of shorter chain lengths will vary slightly, but these differences are inconsequential when considering the overall efficiency of milk synthesis since lipogenesis accounts for a relatively small proportion of the fat in milk (23).

The energy cost of triglyceride synthesis from dietary, depot, or de novo synthesized fatty acids can be calculated with a greater precision. Formation of 1 mole of triglyceride requires 7 or 8 moles of ATP, depending on whether the glycerol phosphate originates from phosphorylation by glycerol kinase or by recycling of enteric or adipose tissue glycerol via hepatic glucose formation and the action of glycerol phosphate dehydrogenase (24). The cost of triglyceride synthesis is therefore about 600 kJ/mol, which represents an efficiency of slightly in excess of 98% (8).

In Table 2 the overall biochemical efficiency of human milk synthesis has been calculated for a milk of representative composition (7.0 g lactose, 1.2 g protein, 4 g fat, 304 kJ gross energy per 100 ml) using different assumptions for the proportion of de novo fatty acid synthesis. The lower assumption of 12% synthesis was derived from the fatty acid profile of milk from well-nourished women (6) assuming that only fatty acids C14 and below were synthesized. The higher value of 36% synthesis was derived from the profile of milk from Tanzanian women on a very low fat diet (6) and assuming that 50% of C16 fatty acids were synthesized in addition to the shorter chain lengths.

Using these biochemical calculations, the overall efficiency of synthesizing just the proximate constituents of human milk falls in the range of 91–94%. This is a very high level of efficiency arising from the fact that most of the fat is assumed to be transferred from the diet even if it is recycled (at a low

Table 2 Summation of the biochemical costs of synthesizing the major milk constituents

Constituent		Concentration (g/100 ml)	Gross energy[a] (kJ/100 ml)[c]	Efficiency[b] (%)	Cost of synthesi (kJ/100 ml)
Lactose		7.0	120	95	126
Protein		1.2	28	88	31
Fat:	A 12% synthesized	0.48	19	73	26
	88% transferred	3.52	137	98	140
	B 36% synthesized	1.44	56	73	77
	64% transferred	2.56	100	98	102
Total:	Assumption A		304		323
	Assumption B		304		336

[a] Calculated from gross energy values of 17, 23, and 39 kJ/g for lactose, protein, and fat.
[b] Derived as in text. Value for synthesized fat includes reesterification costs.
[c] 4.184 kJ = 1 kcal.

biochemical cost) through adipose tissue. If almost all fat had to be synthesized, as it does in ruminants, the efficiency would be about 82% for milk of this composition. It is important to reemphasize that these estimates must represent the absolute maximum efficiency, being derived as they are from a gross simplification of the pathways involved. They make no allowances for nutrient transfer costs, for activation of alternative pathways necessary to match the plasma supply of nutrients to the mammary gland's requirements, or for the costs of synthesizing and transferring the minor constituents of milk. They also take no account of the extra Na/K-ATPase activity on the basolateral membrane necessary for maintaining intracellular and milk ionic balance, for the extra cardiac work necessary to perfuse the gland, or for a number of other minor processes associated with lactation.

The above calculations were based on the use of substrates already assimilated from the diet and available from the circulating, hepatic, or adipose tissue pools. Allowances must also be made for the further costs associated with digestion, absorption, interconversion, transport, and storage of the dietary fuels and protein. These costs can best be assessed from direct measurements of postprandial thermogenesis. Most studies report that 6–14% of the energy from a mixed meal is dissipated as heat (17). Illingworth et al (15) reported a significant 30% diminution of postprandial thermogenesis in lactating women when compared to bottle-feeding controls. They attributed this to increased mammary insulin sensitivity favoring milk lipogenesis at the expense of maternal storage or oxidation. This explanation seems unlikely since the costs of lipogenesis are higher than those of storage. They also report much lower total levels of thermogenesis than most other workers (only 2–3.5% of energy dissipated), which may be a result of the short duration of their postprandial measurements. However, accepting that their demonstration of reduced thermogenesis during lactation is correct, and using this to modify 24-hour estimates of thermogenesis (17), we can assume that about 8% of any extra metabolizable energy ingested to support lactation will be wasted in the process of absorption.

Adding this cost to the biochemical estimates for synthesis, one can calculate that, except when the maternal diet has a very low fat content, producing 750 g of milk with a gross energy content of 2340 kJ would require 2700 kJ of metabolizable energy, or approximately 2830 kJ of dietary energy. This gives an overall food-to-milk-energy conversion efficiency of about 83%, which lends strong support to the FAO/WHO/UNU (10) assumption of 80% in spite of the crudity with which the latter estimate was derived.

CALORIMETRIC EFFICIENCY Metabolic balances, including calorimetric measurements of the maternal maintenance requirements, offer an alternative approach to the theoretical calculations of biochemical efficiency outlined above. Calorimetric efficiency of milk production is usually quoted as

$$\frac{\text{Gross energy in milk}}{\text{Metabolizable energy in excess of maintenance needs}}$$

where the denominator is the sum of excess energy derived from the diet and by mobilization of body fat stores (3). Note that the use of the term "maintenance needs" in this context does not refer to basal metabolism but encompasses all components of expenditure, including physical activity.

Table 3 summarizes the measured efficiencies for a number of animals. Unfortunately, most estimates have been made in dairy cows, and there are few data available from other species. The range of reported efficiencies is relatively small at 57–76%. However, the table needs qualification. Firstly, several of the values do not represent true calorimetric efficiencies since they were derived by estimating, rather than measuring, the maternal maintenance needs. This is less critical in high-yielding animals such as the dairy cows since the milk energy output is usually of the same order of magnitude as the maternal maintenance requirements, and minor alterations in the latter have little impact on estimated efficiency. The confidence limits associated with such measurements in cows are therefore much narrower than those for human lactation, in which a 10% change in maternal requirements is equivalent to 50% of the energy content of the milk.

Secondly, the estimates are heavily dependent on the conditions of measurement. For instance, in cows the efficiency peaks when the molar proportion of acetic acid in the rumen liquor averages 50–60% of total volatile fatty acids (3). Lower concentrations depress efficiency by reducing the fat content of the milk, and higher proportions favor deposition of body fat. Lactational efficiency also varies with the state of maternal energy balance since mobilized body energy is used more efficiently than dietary energy,

Table 3 Calorimetric efficiencies of milk production in a number of species

	Calorimetric efficiency[a] (%)	Reference
Ruminants		
Dairy cow	72	3
Dairy cow	70	3
Dairy cow	67	13
Nonruminants		
Rat	57–58	32
Rabbit	76	26
Pig	85	19

[a] Expressed as Milk Energy ÷ Metabolizable Energy in excess of maintenance.

which is in accord with theoretical predictions based on synthetic versus transfer costs for fats. The efficiencies of conversion of dietary and body energy have been calculated as 63 and 84% respectively in the diary cow (13), and 74 and 94% in the rabbit (26). This difference is likely to be much less pronounced in humans since the high fat content of the diet removes the need for substantial lipogenesis.

Blaxter (3) pointed out that calorimetric efficiencies are usually lower than biochemical efficiencies. For instance, biochemical calculations indicate an efficiency of about 80% for the cow compared to the observed maximum of 72%. This is entirely to be expected from the known omissions in the biochemical estimates, and the two methods can therefore be considered to be mutually corroborative.

On the basis of the data in Table 3 and by extrapolation of the generalized observation that calorimetric efficiency is usually 10–15% lower than theoretical calculations, it seems most unlikely that human lactation can exceed 80% efficiency for the dietary-to-milk-energy conversion; a value of 75–80% is more likely. The frequently reported estimates of apparent efficiencies in excess of this range (21, 36) and sometimes in excess of 100% (R. G. Whitehead, personal communication) can therefore only be explained by changes in the denominator term caused by energy-sparing adaptations in the maternal maintenance requirements.

MECHANISMS FOR MEETING THE ADDITIONAL ENERGY COSTS

Increased Food Intake

Very few studies have made longitudinal measurements of food intake in well-nourished lactating women and included either pre-pregnant or post-weaning baseline measurements (30). Black, Wiles & Paul (1) reported an increment of 2050 kJ/day in months 2–4 of full lactation compared to measurements made 3–6 months post-weaning in 56 women from Cambridge, United Kingdom.

These data can be supplemented by comparing the mean intakes from different groups of lactating and nonlactating women from affluent societies if one first assumes that large sample sizes will average out differences in maternal weight, physical activity, and methodology. The mean intake from nine appropriate studies of nonpregnant, nonlactating women was found to be 8.05 MJ/day, and the intake from 13 studies of lactating women was 9.90 MJ/day; the average increment was 1.85 MJ/day (30). This is very close to the recommended increment of 2.1 MJ/day (10) and indicates that when food availability is unrestricted women do on average meet most of the additional costs of lactation by increasing their intake. This general conclusion cannot, however, be extended to cover individuals since the range of incremental intakes in our Cambridge studies was from −1.3 to +3.8 MJ/day.

If assessed on an absolute basis the mean intake for lactating women of 9.9 MJ/day would appear to be inadequate when compared to the recommended intake of 12.3 MJ/day for women with light activity patterns (10). This has often been misinterpreted as indicating either energy deficiency or an extraordinary level of metabolic efficiency during lactation. In fact, the low intakes can be explained if an appropriate lactational increment is added to the very low energy requirements for maintenance due to modern inactive lifestyles (28). The 22 studies reviewed above were all published after 1970, and a similar review of 18 studies published prior to 1970 yields mean values almost 2 MJ/day higher in each group (30). Recognition of this change in baseline resolves most of the discrepancies between predicted requirements and observed intakes in well-nourished women eating ad libitum.

Utilization of Body Fat Stores

Mammals have adopted a diverse range of strategies in relation to their use of body fat stores in support of lactation. At one end of the range, certain seals remain on land and eat nothing during lactation, thus supporting the entire costs of milk synthesis and maternal maintenance from their fat stores. The other end of the range is represented by species such as mice and rats with large, fast-growing litters. In these species the demands of lactation are so large that they must be met by a substantial increase in food aquisition. Although such species are usually in negative energy balance, the contribution of body fat to the total costs of lactation is quantitatively negligible (30).

It is difficult to judge the position of human lactation in this continuum. As already indicated, the energetic stress of lactation per unit time is extremely low, and this is coupled with large subcutaneous fat deposits that are further increased by fat storage during pregnancy. A large proportion of the energy costs of human lactation could therefore be derived from adipose tissue. However, this appears not to be the normal strategy under conditions of unrestricted food intake.

Table 4 summarizes available data on postpartum weight losses in groups of lactating and nonlactating women in affluent societies. On average the lactating women lost rather little weight (averaging 0.7 kg/month) and their rate of weight loss was no greater than the nonlactating women, although the latter may have been influenced by some intentional dieting (22). These data refute the widely held assumption that human lactation is naturally associated with rapid catabolism of fat stores. The original evidence for this assumption came from a number of sources. Firstly, there has long been an a priori assumption that the extra fat laid down during pregnancy must be intended to supplement lactation, an assumption incorporated into the WHO energy recommendations (10). Secondly, there is abundant evidence from a number of animal species of reciprocal changes in the lipogenic activity of mammary and adipose tissue (37). During lactation lipogenesis tends to be markedly suppressed in adipocytes by a reduction in the number and sensitivity of insulin receptors, by a depression in the activity of lipoprotein lipase and fatty acid synthetase, and by a reduction in the rate of fatty acid reesterification (37). Rebuffe-Scrive (31) has also demonstrated increases in the lipolytic activity of femoral adipocytes in women during lactation. However, although these changes all tend to shift the equilibrium away from fat deposition and to potentiate catabolism, they do not necessarily imply that it must occur; in conditions of abundant food supply it appears that increased food intake largely overrides their effects.

It is probably more realistic to view women's large adipose tissue stores as an emergency buffer against acute restriction of food intake. A prime example of it functioning in this way occurs in rural women in The Gambia, West Africa (27). During the preharvest season, food shortages combine with high levels of agricultural work to cause moderately severe negative energy balance. At this time of year lactating women mobilize significantly more body fat (up to 2 kg/month) than nonlactating women (27). However, during the

Table 4 Postpartum weight loss in well-nourished women

Reference	Lactating (kg/month)	Nonlactating (kg/month)
English & Hitchcock (9)	1.3	1.5
Thomson, Hytten & Billewicz (36)	1.2	1.1
Naismith & Ritchie (22)	0.4	0.7
Manning-Dalton & Allen (21)	0.7	1.2
A. A. Paul, unpublished	0.6	—
A. M. Prentice, unpublished	0.3	—

harvest season all lactating women gain substantial amounts of fat, which again indicates that the mechanisms tending to favor adipocyte lipolysis can be overriden and are secondary to changes in food intake.

The above discussion for group mean values should not obscure the fact that in any group there is a wide between-subject variability in the proportion of energy derived from diet or from body stores. Combined data from two studies performed in Cambridge revealed a significant reciprocal relationship between postpartum weight changes and the incremental energy intake during lactation ($r = -0.55$, $n = 56$, $p<0.001$) (A. A. Paul and A. M. Prentice, unpublished). (The increment was calculated relative to the intake in pregnancy because of the long interval before the post-weaning measurements could be made.) The mean increase in food intake was 1090 kJ/day and mean weight loss was 17.4 g/day, equivalent to 530 g/month. The least-products regression line has a slope of 30 g/1000 kJ, which is not significantly different from the expected energy density of weight changes. The intercept at zero weight change predicts that an energy increment of 1950 kJ/day would be necessary to maintain energy balance. Since the intake during pregnancy averaged 750 kJ/day higher than in the nonpregnant state, the total required increment would be 2700 kJ/day. This value exactly matches the predicted cost of synthesizing 750 g of milk at 290 kJ/100 g and with an efficiency of 80%.

Our Cambridge data illustrates the wide range in physiological strategies selected by individual women who were free to choose their incremental intake without external constraints. The changes in food intake ranged from −1300 to +3790 kJ/day and in weight from −6.1 to +4.0 kg assessed over a two-month period. Manning-Dalton & Allen (21) and Butte et al (4) have observed similarly wide ranges with the same reciprocal relationship between the two variables. Unfortunately, none of these studies have been able to identify the factors that cause women to choose a particular strategy. In the relatively short periods of lactation encountered in most Western communities this may not matter since in our data we could detect no association between lactational performance and incremental energy intake, i.e. the source of the extra energy was immaterial. However, when lactation is prolonged there is a limit to the amount of body fat that can be utilized, and an eventual inhibition of lactation must occur if food intake does not increase.

Energy-Sparing Adaptations

Many studies from the developing world have demonstrated that lactation can be sustained under very harsh dietary conditions (27), and even if the exact caloric intakes recorded have been underestimated there is no doubt that there is a strong drive toward milk synthesis. These findings have encouraged a search for energy-sparing adaptations that operate during lactation. The maximum likely efficiency of the milk synthetic process itself has been analyzed above. There are three remaining components of the total energy budget in which some energy could be spared: basal metabolic rate (BMR), thermogenesis, and physical activity.

On purely theoretical grounds basal metabolic rate might be expected to rise during lactation since human milk synthesis is essentially a continuous process and liberates approximately one sixth of the total synthetic cost as heat. An increase in BMR of approximately 400 kJ/day would therefore be expected in an average woman. However, if the heat liberated during milk synthesis can be put to useful work by replacing another component of heat production necessary for thermoregulation this increment may not be observed. Similarly, there might be a reduction in maternal protein turnover or energy substrate cycling that would offset the anticipated rise in BMR.

In practice there appears to be no consensus in the literature as to whether BMR increases, remains the same, or decreases in human lactation. Many studies of lactating women contain no control measurements in nonpregnant, nonlactating subjects and can only be judged by comparison against predicted BMRs for women of the same height and weight. A review of all such data published this century concluded that it provided some evidence for an actual reduction in BMR during lactation (30). In particular a study by Rowe & Boyd (34) appears to have been well designed with a large sample size. BMR showed a U-shaped depression coincident with peak lactation; the minimum value was 15% below the Harris-Benedict predictions. Similar results were reported by Blackburn & Calloway (2), who made resting metabolic rate (RMR) measurements in 13 lactating women at 8–12 weeks postpartum. On average their RMRs were 23% lower than values predicted using the standard formulae.

More recently, a number of prospective studies have made longitudinal measurements of basal metabolism during lactation and in the nonpregnant, nonlactating state. A. Sadurskis, E. Forsum, and J. Wager (unpublished abstract) observed a 9% increase at two months of lactation (compared to pre-pregnant values) in 22 women who were 3.4 kg heavier than their pre-pregnant weight. Illingworth et al (15) found no difference in RMR when measured during lactation and postlactation, or when cross-sectionally compared with bottle-feeding controls. In contrast Whitehead et al (38) demonstrated that RMR remains 5% lower than the pre-pregnant level during the first year of lactation in rural Gambian women, and we have observed a significant reduction of 490 kJ/day in well-nourished lactating women compared to postlactation measurements (A. M. Prentice, unpublished).

On balance therefore, there is more evidence to suggest that metabolic rate is decreased during lactation than there is to suggest an increase. Although the extent of the decrease is usually small (up to 500 kJ/day) it should be viewed in the context of a predicted increase, and may represent an overall effective saving of up to 900 kJ/day.

The second potential compartment in which energy-sparing adaptations could occur is thermogenesis. Since this compartment represents only 10% of total expenditure, any savings are likely to be small. The only study addressing this topic was reviewed in the section on biochemical efficiency. It recorded a predicted saving of up to 200 kJ/day (15).

The final area where energy could be spared for lactation is physical activity, and the potential savings are entirely dependent on the habitual level of activity in the nonpregnant state. For sedentary affluent women the demands of motherhood may increase energy expenditure. However, for physically active women there is considerable scope for a reduction in expenditure. Women feeding on demand may spend up to 15% of the day feeding their baby. If the cost of sitting and breast-feeding is taken as 6 kJ/min and if this replaces a farming or domestic activity at 15 kJ/min then the energy saved over 12 hours of daylight would amount to nearly 1000 kJ. This, however, is likely to represent a maximum estimate. In practice activity diary studies in Gambian women have tended to observe lower savings (33), and recent measurements using the doubly labelled water method have shown that lactating women spent the same amount of energy on physical activity as nonpregnant controls (35).

In summary, there is evidence that changes in maternal processes can spare energy, but the absolute maximal savings are likely to be 900 kJ/day from basal metabolism, 200 kJ/day from thermogenesis, and 1000 kJ/day from physical activity, giving a total of about 2000 kJ/day. A more realistic estimate under most circumstances would be substantially less than this; probably between 500–1000 kJ/day.

MECHANISMS FOR SUPPLYING APPROPRIATE SUBSTRATES TO THE BREAST

In many animals, particularly high-yielding ruminants, the demands of the mammary gland for glucose, acetate, lactate, or amino acids as the substrates for milk synthesis are greater than the requirements of the maternal compartment itself (37). Under such circumstances profound homoeorhetic adjustments are necessary. However, simple calculations demonstrate that these are unlikely to be necessary in an adequately nourished woman. At peak lactation, average production of protein, fat, and lactose is approximately 9, 30, and 56 g/day. Assuming that 20% of fat is synthesised de novo from glucose this would decrease the fat requirement to 24 g and give a total glucose requirement of approximately 75 g/day. In a woman consuming 10 MJ/day with a protein:fat:carbohydrate content of 14:40:46 calculated by energy, the requirements for lactation would represent only 11, 23, and 26% of daily intake respectively.

CONCLUSIONS

In most mammals the relative costs of lactation are so high that they must be met by a very substantial increase in food intake, and there is a close dose-response relationship between dietary intake and milk yield. This is not the case for human lactation since the combination of a very low stress per unit time and large energy reserves provides women with a unique flexibility in which the additional costs can be met from the diet, from body fat, and to a certain extent by energy-sparing metabolic adaptations. As a consequence, human lactation is remarkably resistant to acute caloric insufficiency and appears only to be compromised by severe or long-term starvation (29). However, when the maternal diet is inadequate, the mother's own nutritional status will suffer. There is therefore no reason to modify the traditional view of human lactation as a risk period in which special attention should be given to maternal diet.

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