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# 4

## Lactation, Energetics, and Postpartum Fecundity

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The last two decades of the twentieth century have witnessed a dramatic growth in the field of human reproductive ecology, resulting in a better understanding of variation in human fertility patterns related to changes in ecological context. The first, and perhaps most significant, advance in this area was the recognition of the suppressive effects of lactation on postpartum fecundity. It is now well established that lactation is the major determinant of the period of postpartum infecundity. As a result of this recognition, lactation plays a preponderant role in any discussion of variation in natural fertility patterns (Wood 1994). Many studies have shown the great variety of social and physical environments in which lactation occurs, as well as the variability in the response of female reproductive physiology. However, the proximate mechanisms underlying the phenomenon of lactational infecundity are still not clear. The aim of this chapter is to summarize the information available on lactation and postpartum fecundity and to present the current debate surrounding how the suppressive effects of lactation are mediated. After a brief introduction to the costs and benefits of breastfeeding, we concentrate on the links between lactation and postpartum fecundity. A historical overview describes the context in which the current ideas evolved and sets the stage for the presentation of the two leading hypotheses aimed at identifying the proximate causes of lactational infecundity. Although focused on mechanisms, these two hypotheses also have implications for the functional interpretation of lactational amenorrhea. We conclude with the presentation of data from our research of lactating Toba women of northern Argentina as a case study that allows us to confront the predictions of the two competing hypotheses.

### THE ENERGETIC COSTS OF BREASTFEEDING

As with pregnancy, the lactating mother is, at least during the exclusive breastfeeding period, "metabolizing for two." In mammals, unlike other animals, the *direct* physiological investment of the female does not finish when the infant is born. The mother continues diverting certain amounts of her own available energy to her offspring until the moment of complete weaning. If we measure this investment in terms of calories it becomes clear that the process of lactation represents a considerable energetic burden. In human females, the average energy cost of the milk produced during the period of exclusive breastfeeding is approximately 500 kcal/day. Taking into account the efficiency of conversion of dietary energy to milk energy (approximately 80%), the total average cost can be estimated as 625 kcal/day (Dewey 1997). In cases of inadequate dietary intake this could represent as much as 50% of the mother's energy budget.

In order to meet the cost of milk production, a breastfeeding woman can increase the energy intake, mobilize fat reserves, reduce her energy expenditure, or any combination of these strategies. Well-nourished lactating mothers generally increase food consumption, particularly during the early postpartum period (Goldberg et al. 1991). However, for most populations in the developing world where inadequate diets are the norm, this option is not often feasible. Mobilization of fat reserves seems to be the most utilized mechanism for meeting the cost of lactation. Although there is substantial variability, on average, lactating women lose about 500 g/month of body weight. This weight loss could be taken as an indication that body fat reserves are indeed being mobilized to support lactation (Dewey 1997; Prentice et al. 1996). The third strategy would be to decrease the energy expenditure during the exclusive breastfeeding period. This could be achieved through reductions in basal metabolic rate (BMR), dietary-induced thermogenesis (DIT), or physical activity level (PAL). The basal metabolic rate seems to be unchanged or slightly increased during lactation (Goldberg et al. 1991; Singh et al. 1989). Studies examining changes in DIT during lactation have shown mixed results. Given that DIT contributes only about 10% of the total energy expenditure, even if there were changes in DIT they could only account for a minimal proportion of the total energy balance (Dewey 1997). There is a great variation in PALs during lactation depending on the ecological context of the woman. In affluent populations, PALs are slightly lower during the early postpartum period than during the non-pregnant/non-lactating period (Dewey 1997). In contrast, little difference in activity levels among women in different reproductive states has been found in developing world populations (Guillermo-Tuazon et al. 1992; Vinoy et al. 2000). Many times, lactating women cannot afford to cut back their level of activity and, hence, their contribution to family subsis-

tence. In sum, women in different ecological contexts seem to use different strategies to balance the energy costs of lactation. These strategies are not mutually exclusive; they can be taken as complementary ways of saving energy. Even within the same population, there seems to be a significant variability in the type of energy-saving alternative utilized (Goldberg et al. 1991).

### THE BENEFITS OF BREASTFEEDING

The contributions of lactation to infant survival and maternal health are manifold. Detailed accounts of the effects of breastfeeding on maternal health have been published by others (Heinig and Dewey 1997; Stuart-Macadam 1995) and are beyond the scope of this chapter. We will briefly describe three major contributions of breastfeeding to the mother's fitness (understood here as reproductive success). The most obvious is the nutritive function of breast milk. Breasts secrete a rich, dynamic substance capable of completely nourishing an infant for the first six to nine months of life. The energy density of breast milk depends mainly on its fat and lactose content. In well-nourished populations, fat contributes about 50% of the total milk energy; milk lactose adds 40% to 45%, whereas proteins contribute the rest (Dewey 1997). Although it is difficult to obtain an accurate estimate of the energy density of breast milk, the average gross energy content is generally reported to be about 0.68–0.74 kcal/g (Prentice et al. 1996). Milk fat or lactose concentrations vary very little during lactation, but they can be affected by maternal body composition. Field studies (Brown et al. 1986; Perez-Escamilla et al. 1995; Prentice et al. 1981) revealed a positive correlation between milk fat and estimations of total maternal body fat. In populations that practice on-demand breastfeeding, infants generally compensate for differences in energy density by consuming higher or lower volumes of milk (Perez-Escamilla et al. 1995).

The second major contribution of breastfeeding to the infant's survival is the immunological protection breast milk confers, mainly during the critical initial months. Throughout the world, breastfeeding is associated with significant prevention of infant mortality and morbidity (Cunningham 1995). The infant's own immune system is not fully developed and will not be for several months. The infant relies on its mother's supply of antibodies, transferred via colostrum and breast milk, to fight viruses, bacteria, and other parasites. In addition to this form of passive protection, breast milk is also rich in regulatory substances that stimulate the development of the infant's own secretory immune system. By reducing the exposure to external pathogens (microbial or allergenic) present in other fluids or foods, breastfeeding also lowers risk of gastrointestinal infections, respiratory

illnesses, bacteremia, and meningitis (Cunningham et al. 1991). In rural or marginal populations this could be crucial since people often lack the opportunities to obtain uncontaminated water necessary to prepare powdered formula. Many studies point also to the benefits of breastfeeding for the long-term development and health of the infant. As an example, there is evidence for an association between early feeding practices and coronary pathologies, disorders of immune regulation, and psychomotor development (Cunningham 1995; Lucas 1998).

The fertility-reducing effects of lactation are beneficial for both the mother and her current and future offspring. In breastfeeding mothers the return to full postpartum fecundity is usually delayed several months. By extending the interbirth interval, lactation prolongs the period during which a given child benefits from breast milk, and lactation also contributes heavily to its survival and that of its siblings. It is now well established that closely spaced births, in other words, less than 2 years apart, lead to an increased rate of infant mortality, not only of the first born child in a sequence but also of the second (Mozumder et al. 2000). For example, Hobcraft et al. (1983) found that in 13 of 23 countries, a birth in the 2 years prior to the birth of the index child increases that child's risk of dying by more than 50%. In a study conducted in Guatemala, fetal asymmetric stunting or wasting was related to short interbirth intervals (Neel and Alvarez 1991).

In addition to the disadvantages for the offspring, the mother's energy supply may be severely affected by closely spaced births. A lactating woman who becomes pregnant while her infant is still young is burdened with the task of metabolizing for three, at least until the infant is completely weaned. Trying to meet those increased energy requirements will compromise her nutritional status and have a negative impact on her own health as well as her offspring's. The "maternal depletion syndrome" was first suggested by Jelliffe and Maddocks (1964). This syndrome is characterized by a progressive reduction in the female fat reserves and lean tissue with successive births and periods of lactation. If a woman consumes only the amount of protein recommended for non-pregnant/non-lactating women, she loses about 19% of her lean tissue (Dewey 1997). This syndrome is particularly notorious in developing countries where poor nutritional states and high female workloads are the norm. The Au women of Papua New Guinea, for example, show both a short-term decline in adiposity following childbirth and a long-term fertility-related decline (Tracer 1991). Low energy reserves can lead to low birth weights (Rodriguez et al. 1991; Tontisirin et al. 1986), intrauterine growth retardation (Bhatia et al. 1984), and premature labor (Khanna et al. 1977).

From an evolutionary perspective, we can say that female physiology has been shaped by natural selection to produce a fluid that both nour-

ishes and protects her offspring. At the same time, by exerting its contraceptive effects, lactation helps to keep sufficient time between periods of increased metabolic requirements (gestation and lactation) and, hence, contributes greatly to the female's overall reproductive success.

## LACTATION AND POSTPARTUM FECUNDITY

The fact that a lactating woman was less likely to be menstruating than a non-lactating one was commonly recognized from antiquity to the eighteenth century. However, the contraceptive effect of lactation was considered little more than an "old wives' tale" by western physicians in the late nineteenth and early twentieth centuries. Clinical studies demonstrated that there was indeed a period of amenorrhea following parturition, but it was not clear whether it was a refractory effect of gestation or a direct effect of lactation (Gjoiosa 1955; McKeown and Gibson 1954; Sharman 1951).

In 1961, the French demographer Louis Henry published a seminal paper focused on the natural variation in human fertility and the proximate causes of that variation. An important hallmark of his work is that he turned attention away from *sociological* explanations and proposed *physiological* causes of variation in natural fertility. In his analysis, he found that the period of postpartum subfecundity was highly variable among populations, but that the current sociological explanations that implied postpartum sexual taboos in traditional societies could not account for that variability. He suggested that variation in the resumption of ovulation after childbirth might be the most important source of variation in interbirth intervals. The evidence available at that time indicated that women who lost a child at birth, and therefore never breast-fed, resumed menstruation earlier than those who did breast-feed. With that evidence in mind, Henry reckoned that the practice of lactation might be related, by some unknown mechanism, to the resumption of postpartum ovulation. However, he also recognized that the relationship between lactation and resumption of ovulation was not a simple one. He proposed that understanding the physiological factors that govern that relationship could "help us to understand why there exist among populations such variability in natural fertility" (Henry 1961).

### The "Nursing Intensity" Hypothesis

Describing the proximate mechanisms that could account for the variation in the duration of lactational amenorrhea became a central problem for testing Henry's hypothesis. Reproductive biologists interested in solving this puzzle faced two different but intimately related problems: finding

the neuroendocrine pathways that link the physiology of lactation with the physiology of reproduction, and finding what "observable" component of lactation was responsible for its suppressive effects on female fecundity. The first quest proved to be a difficult one, and to date a clear understanding of the neuroendocrine control of lactational infecundity remains elusive.

Early studies on the matter focused attention on *prolactin* as the primary hormone suppressing ovarian function. From clinical research, it was known that a pathological condition by which prolactin levels in blood are excessive was associated with ovarian dysfunction. Hyperprolactinemia is often treated with bromocriptine, a dopamine agonist that inhibits prolactin. This treatment causes a reduction in prolactin levels and a resumption of normal ovarian cycles (Robyn et al. 1976; Sartorio et al. 2000). Other studies with nursing women showed considerably high levels of prolactin throughout the period of amenorrhea and decreasing levels about the time of resumption of menses (Delvoe et al. 1976; Howie and McNeilly 1982; Wood et al. 1985). Tyson (1977) analyzed changes in prolactin levels in much more detail. Within minutes of the infant latching on to the nipple, prolactin levels increase dramatically. Then, soon after the infant stops nursing, prolactin levels slowly drop. Tyson's data suggested that the temporal pattern of suckling could be of importance in unmasking the link between lactation and ovarian function. A mother nursing her infant with sufficient frequency could maintain high levels of prolactin, which, in turn, could inhibit ovarian function.

The actual mechanism by which prolactin could suppress ovarian function remained unclear, despite the enthusiasm that this idea generated. In vitro studies performed by McNatty and colleagues (1974) indicated that high levels of prolactin in cultured granulosa cells were associated with a reduced ability of each cell to produce estradiol and with an inhibition in the secretion of progesterone. This study was strongly criticized, among other reasons, because prolactin receptors could not be found on granulosa cells (McNeilly et al. 1982). In recent years the contraceptive role of prolactin was called into question by several studies (McNeilly 1993; Schallenberger et al. 1981). As a result, it is now believed that prolactin is not directly involved in the system linking lactation and ovarian quiescence. Other mechanisms are being explored, most of them centered on the factors that might affect the pulsatile secretion of Gn-RH from the hypothalamus (Wood 1994). The current view of the neuroendocrine control of lactational infecundity is highly speculative, and more research is expected to settle some controversial relationships.

At another level of analysis, researchers began to investigate which aspects of the mechanics of lactation were associated with the period of

amenorrhea. At the time when prolactin was the best candidate as suppressor of ovarian activity, Delvoe et al. (1977) presented data from a natural fertility population in Zaïre providing evidence of the relationship between nursing frequency and prolactin levels. In their study, prolactin levels in mothers who nursed three times a day or less fell within the range of values typical of non-pregnant, non-lactating women within six months. In contrast, prolactin levels in women who nursed six times a day or more were three times higher at six months. In 1980, Konner and Worthman published their study of nursing patterns and ovarian function among the Kung San of the Kalahari Desert. Kung San mothers nursed their infants very frequently, averaging 4 bouts per hour. Nursing bouts lasted, on average, 2 minutes, and they were separated by 13 minutes. This high frequency was maintained for the first two years of the infant's life. They inferred that such an intensive pattern would maintain high prolactin levels (although these were never measured), which in turn would exert a suppressive effect on the mother's fecundity, accounting for the 44-month interval between births. These results, coupled with Tyson's analysis, pointed to the centrality of the temporal arrangement of suckling events for modulating ovarian function.

So important appeared to be the choreography of nursing that it served as the basis for the postulation of a major hypothesis aimed at explaining the fertility-reducing effects of lactation. This hypothesis proposes that the "intensity" of nursing is a major controller of the duration of lactational infecundity. Although hard to operationalize initially, the intensity of nursing was then defined as a combined measure of suckling frequency, duration of the suckling bout, and total duration of nursing. The evidence suggested that either a high frequency of nursing or few nursing episodes of long duration were effective in preventing ovulation. Perhaps the most influential study that focused on this issue was the one conducted by McNeilly, Howie, and colleagues at the University of Edinburgh (Glasier et al. 1983; Howie et al. 1982a, 1982b; McNeilly et al. 1982). The researchers followed 27 breastfeeding mothers and 10 women who bottle-fed their infants from birth. Urine samples were collected weekly for estimation of estradiol and progesterone. Every two weeks, blood samples were collected for determination of prolactin levels. The results indicated that nursing behavior and ovarian function were indeed associated. Those mothers who resumed ovulation during the period of lactation (13 of 27) had reduced nursing frequency to less than 6 bouts/day, total nursing time to less than 60 minutes/day, and had introduced at least two supplementary feeds per day. The authors stressed the importance of the timing of introduction of supplementary feeds as starting point of the changes in nursing behavior and reproductive physiology. They argued that when supplements are

introduced, women change their breastfeeding behavior to a pattern of less frequent, shorter nursing episodes. This, in turn, leads to decreasing levels of prolactin, which allowed the resumption of fecundity.

Data from many field studies of natural fertility populations around the world appeared to support the nursing intensity hypothesis (Jones 1989; Panter-Brick 1991; Vitzthum 1989; Wood et al. 1985). The idea was enthusiastically accepted by biological anthropologists and demographers alike, as it seemed to answer Henry's old question about the variation in fertility patterns. According to the nursing intensity hypothesis, variation in the duration of lactational infecundity can be interpreted to reflect the wide diversity in nursing behavior across populations: the more intensive the breastfeeding, the longer the impact on fertility. Women in the developing world, with patterns of on-demand breastfeeding, would have longer periods of lactational amenorrhea than women in industrialized societies where breastfeeding, if practiced at all, was much more structured, with long interbout intervals. The nursing intensity hypothesis seemed to make evolutionary as well as demographic sense. Short (1987) argued that, in our formative past, nursing patterns would have been very intensive. Infants would have nursed very frequently, until other foods were introduced. The reduction in nursing intensity as the baby fed on other foods would have been interpreted by the mother's body as a green light for resumption of ovarian activity: "your infant can survive on solids now, it is safe to get pregnant again." Lactation was favored by natural selection, among other things, as a mechanism to prevent dangerously close birth intervals.

### The "Metabolic Load" Hypothesis

The nursing intensity hypothesis held strong until quite recently a number of contradictory results began to accumulate. The first assumption to be questioned was the validity of the physiological bases of that hypothesis. Prolactin per se cannot be considered the cause of reproductive suppression. Furthermore, recent data indicate that prolactin levels do not reflect nursing frequency as tightly as was previously thought. No clear correlation could be found between nursing bouts and prolactin profiles in a study that involved 24-hour video monitoring and blood sampling of nursing mothers housed in a clinical research unit (Tay et al. 1996). There is evidence that prolactin could be maintained at either relatively high (Stallings et al. 1996) or low (Tay et al. 1996) levels without acute response to nursing. Although these findings remove prolactin from its originally leading role, it is quite clear that it is indirectly associated with the period of lactational amenorrhea. Postpartum prolactin levels could be taken as a marker for a physiological state that leads to amenorrhea. Other

field studies also pointed to problems with the nursing intensity hypothesis (Peng et al. 1998; Tracer 1991; Worthman et al. 1993). In these studies, the frequency or the duration of the nursing bout was not predictive of the duration of lactational amenorrhea. It was evident that the variation in the temporal pattern of nursing left a great part of the observed variation in the duration of lactational amenorrhea unaccounted for.

Several studies suggested that maternal condition might be associated with significant variation in the duration of lactational infecundity (for a review see Ellison 1995).<sup>1</sup> Huffman and colleagues (1987) reported the relationship among nutrition, breastfeeding, and postpartum amenorrhea in women of Matlab, Bangladesh. In their sample, women with poor nutritional status in the first months postpartum resume menses later (at 20.2 months) than those showing a better nutritional status (at 15.5 months). Data from another impressive longitudinal study conducted in The Gambia also suggested that maternal energetics play an important role in the resumption of postpartum fecundity (Lunn et al. 1984). In this study, maternal dietary supplementation during pregnancy and lactation, and lactation alone, was associated with a decrease in the duration of lactational amenorrhea relative to that observed in mothers who did not receive dietary supplements.

In light of these findings, an alternative explanation for the great variation in the duration of lactational amenorrhea can be proposed (Lunn 1992; Ellison 1995, 2001). The argument behind this new hypothesis is that the intensity of suckling reflects the energetic stress that lactation represents for the mother. The attention is now shifted from the suckling stimulus per se to the *relative metabolic load* of lactation, in other words, the proportion of the mother's energy budget that is devoted to milk production. In this context, the variable effects of lactation on postpartum fertility may depend on the relative metabolic burden that lactation poses on the mother. The higher the relative metabolic load of lactation, the longer the period of lactational infecundity. Maternal condition would then contribute to the contraceptive effects of lactation. Lactation would represent a higher relative metabolic load for poorly nourished mothers than for well-nourished ones. Exclusively breastfeeding a young infant poses a higher metabolic stress than breastfeeding an older baby who had begun to be fed on semi-solids or solids.

### Comparing Hypotheses

The metabolic load hypothesis explains the previous findings on the contraceptive role of lactation as well as the nursing intensity hypothesis. However, a problem soon becomes evident when one tries to differentiate the predictions of the two hypotheses. Under most circumstances, nursing

intensity is a strong predictor of relative metabolic load. Hence, the principal explanatory variables are often confounded. Available data come mainly from two different settings: clinical studies and field studies. The clinical studies provided information on the response of mainly well-nourished women practicing some form of scheduled nursing (Diaz et al. 1988; Heinig et al. 1994). In these women, the mean duration of lactational amenorrhea is relatively short (6.3 months). The explanation provided by the nursing intensity hypothesis seems satisfactory: there is an early resumption of ovarian activity because nursing frequency is low and/or the intervals between nursing bouts are long. The metabolic load hypothesis would also be valid since the shorter period of amenorrhea might be the result of a lesser energetic stress that lactation implies for women in good nutritional status. Studies conducted among traditional societies (see Ellison 1995 for a review) usually show the other extreme—the period of lactational amenorrhea in poorly nourished women practicing intense nursing is relatively long (mean = 20 months). Again, both hypotheses explain the results equally well.

The vast majority of studies published to date focused on breastfeeding women that were either (a) well-nourished with low nursing intensity (clinical studies) or (b) undernourished with high nursing intensity (field studies). In order to confront the predictions of the two hypotheses, we would need to study women for whom both nursing intensity and energy availability are high, or vice versa. We are currently working with one of those populations. In 1997, we started the Toba Reproductive Ecology Study in the province of Formosa, Argentina. The communities we are currently working with provide an excellent opportunity for evaluating the factors affecting the duration of lactational amenorrhea.

#### LACTATIONAL AMENORRHEA AMONG TOBA WOMEN

The Toba are one of eight ethnic groups currently inhabiting the Argentine Chaco (Braunstein and Miller 1999; Martinez Sarasola 1992). Originally seminomadic hunter-gatherers, many groups moved to urban and periurban environments during the past fifty years. These communities depend mainly on the wage labor of men, but most aspects of their traditional life remain deeply rooted.

We are conducting our studies in the village of Namqom, located 11 km north of the city of Formosa (58° 12' W, 28° 10' S). Approximately 2,500 people are distributed in a 100-hectare area. Men are temporarily hired as construction workers in Formosa city or by development programs in the village. Women's activities include household chores, child caretaking, and basket weaving. A few women are employed temporarily as cooks,

teaching assistants, or health agents. Some women go to the city once a week to sell their weavings or medicinal herbs door-to-door.

Namqom has relatively good access to health services, mainly provided by the local health center and the city's hospitals. Women receive free pre- and postnatal care and they are taken to the city hospital for delivery. Family-planning programs are not promoted in this area. Consequently, less than 5% of women use contraceptive methods (mainly oral contraceptives, when they are available at the health center). Complete family size for women in Namqom averages 7.8 ( $\pm 1.2$ ), and the mean interbirth interval is 24.8 months ( $\pm 6.8$ ). Infant mortality is high, with 14% of children born dying before their second birthday. Breastfeeding is almost universal. Toba women breast-feed their children until they are 2–3 years of age, or until the next pregnancy. Cosleeping also allows for on-demand nighttime nursing.

We conducted an observational study of the nursing behavior of 32 mothers, whose babies ranged from 2 to 20 months of age (Valeggia and Ellison 1998). Each mother-infant pair was observed for two 4-hour periods (one in the morning and another in the afternoon) separated by a month interval. Nursing activity was recorded to the nearest second. Although nursing practices can still be considered "on demand," we found a wide variation in the temporal arrangement of nursing periods. Overall, regardless of age of the infant and time of the day, the frequency of nursing events (periods when the infant was on the nipple) averaged 3.1 ( $\pm 1.9$ ) per hour (Figure 4.1a). There was little variation in frequency of nursing during the first year of life; afterwards, it declined slowly. On average, the duration of nursing events did not change with age either (Figure 4.1b). The overall mean duration of nursing events was 2.3 ( $\pm 2.1$ ) minutes. Note that these indices of nursing intensity are close to those

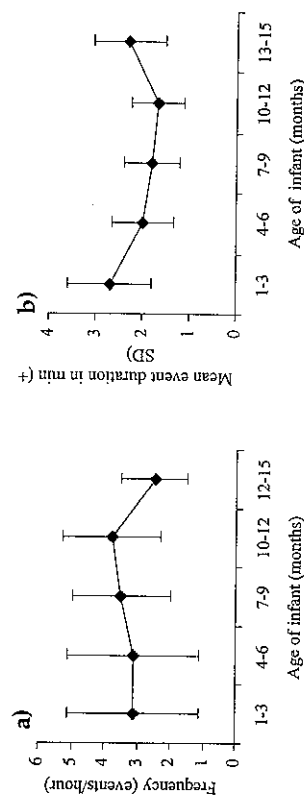


Figure 4.1. Mean frequency of nursing events (a) and mean duration of nursing events (b) for a sample of 70 lactating Toba women.



originally reported for the !Kung (Konner and Worthman 1980). Preliminary results of a follow-up study that involved 70 mother-infant pairs also show an intense practice of nursing with high variability in the temporal pattern among mother-infant pairs and little change in nursing frequency during the first nine months of life.

Toba mothers offer semisolid supplements at 6 to 9 months of age. This is a very gradual process—it generally starts with some broth or soup given during the only structured meal of the day. They offer solid snacks (bread, *torta frita*) only when the baby can sit by itself. The use of bottles and commercial formula was uncommon until very recently.

Lactating Toba women in Namqom are in a state of high energy availability. The typical diet for Namqom villagers is quite monotonous. Early in the morning they prepare *mate*, an herbal infusion typical of the region. Later in the morning women and children may have a cup of sugared milk with a roll of white bread or a round of "*torta frita*," a flour patty fried in oil or lard. The "*comida*," the only structured meal of the day, typically consists of a noodle or rice soup with onions, potatoes, manioc, and yams. In higher income families the soup also contains beef and tomato sauce. During the afternoon and evening, they snack on pieces of bread or *torta frita*. When they can afford it, they incorporate bananas, tangerines, and grapefruit. In general, this diet is highly caloric, very rich in complex carbohydrates and fat, and poor in proteins, iron, and essential micronutrients.

The energy expenditure of Toba women is low to moderate as suggested by behavioral observations of daily activity patterns of 70 lactating women. Women spend most of the day in low energy activities; for example, 70% of daytime was spent sitting while washing clothes, breastfeeding, taking care of the infant, or simply chatting. Only 2% of their time was spent in energetically demanding activities such as chopping wood, carrying loads of water or firewood, or walking long distances.

As a result of a relatively high calorie intake and low energy expenditure, women appear to be well nourished. Table 4.1 shows mean body mass index (BMI = weight/height<sup>2</sup>) by time postpartum for a group of lactating women. The values indicate that most women are heavy for their height, according to international standards. Only two women in our sample of 120 lactating mothers approached the value of 18.5 kg/m<sup>2</sup>, below which an adult is considered undernourished. The BMI values also show that there is no change with time postpartum, which would indicate drainage of maternal fat reserves. Measures of body fat, arm circumference, and skinfold thickness also follow the same trend, suggesting that most of these women have high energy availability.

What would the current hypotheses predict for women in Namqom in terms of the duration of lactational amenorrhea? Given the sustained, intense pattern of nursing, the "nursing intensity" hypothesis would pre-

Table 4.1. Body Mass Index of Toba Breastfeeding Women during the First 20 Months Postpartum

Month Postpartum	N	Mean BMI	s.d.	Range
0	35	26.3	3.0	19.0-32.5
1	57	26.0	3.6	18.8-33.8
2	60	26.0	3.7	18.0-33.0
3	66	25.6	3.6	17.7-33.2
4	62	25.6	4.1	17.7-37.5
5	59	25.1	4.1	17.8-37.8
6	68	25.4	4.5	17.6-37.6
7	60	25.5	4.0	17.8-35.0
8	73	25.5	4.3	17.5-35.3
9	54	26.1	4.5	17.5-36.3
10	63	25.4	4.5	18.0-36.8
11	51	25.6	4.5	18.2-36.6
12	54	25.9	4.4	18.8-36.9
13	40	25.6	4.8	16.9-37.0
14	42	26.6	5.0	18.9-37.9
15	32	26.2	4.3	18.6-37.3
16	29	26.2	3.8	20.2-35.1
17	24	26.1	4.4	18.9-36.3
18	18	26.3	4.5	19.8-37.1
19	13	25.6	5.3	19.0-37.3
20	32	25.0	4.7	18.3-37.4

dict a long period of lactational amenorrhea. According to the "metabolic load" hypothesis, however, given the high energy availability we should expect a shorter period of lactational amenorrhea. A survival analysis based on data from 120 women revealed a mean duration of lactational amenorrhea of  $9.8 \pm 4.0$  months—from birth of an infant to the reported date of first postpartum menses (Figure 4.2). That is a relatively short period of lactational amenorrhea compared with most traditional populations practicing intensive breastfeeding. Furthermore, a preliminary analysis of the temporal pattern of nursing and the return to postpartum fecundity indicates that there is no association between these variables. Even within the same population, the effect of maternal condition on postpartum fecundity seems apparent. Older women, who also have higher parity, tend to have longer periods of amenorrhea than younger ones. Women who were 35 years old or more had an average period of lactational amenorrhea of 12.1 months ( $\pm 5.4$ ,  $n = 12$ ). For the intermediate age category (20 to 34 years old) the mean was 9.7 months ( $\pm 4.2$ ,  $n = 60$ ), while teenagers (14 to 19 years old) averaged 9.0 months ( $\pm 3.9$ ,  $n = 36$ ).

In order to examine the hormonal milieu associated with the return to postpartum fecundity in these women, we are currently analyzing urine

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Month post-partum	% women remaining amenorrheic
1	100
3	95
5	85
7	75
9	65
11	55
13	45
15	35
17	25
19	15
21	10
23	10
25	10
27	10
29	10

Figure 4.2. Survival curve representing percentage of breastfeeding women still amenorrheic by time postpartum.

samples collected weekly from 70 lactating Toba women. These samples are being analyzed for estrogen and progesterone metabolites (E1C and PdG, respectively), prolactin, and c-peptide (a metabolite of insulin). There is mounting evidence showing that insulin plays a crucial role in the integration between energy homeostasis and female reproductive physiology (Brüning et al. 2000; Burks et al. 2000). In addition to its well-known metabolic effects, insulin appears to modulate ovarian function (Franks et al. 1999; Wu et al. 2000) and has been shown to increase gonadotropin-stimulated gonadal steroid production (Poretsky et al. 1999). The association between insulin metabolism and the maturation of the HPO axis during human puberty has been well described (Caprio 1999; Moran et al. 1999). However, the postpartum changes in insulin levels that can be associated with the return to fecundity in women remain virtually unexplored.

Preliminary analyses of urine samples from 70 breastfeeding Toba women indicate that levels of urinary c-peptide increase steadily with time during the first year postpartum (Figure 4.3,  $r = 0.94$ ). In addition, there seems to be a clear difference in insulin metabolism between women who resume menses early (3–6 months postpartum) and those who resume later (12–18 months postpartum). Women with short periods of lactational amenorrhea are characterized by lower c-peptide levels throughout lactation than are women who resume menstruation later. Women with longer periods of amenorrhea also display a drop in insulin values prior to resumption of menses, a pattern that is visible in a plot of aggregate data aligned on date of first postpartum menstruation (Figure 4.4). This pattern

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Time postpartum (months)	ng C-peptide/mg Creatinine
1	10
2	12
3	15
4	18
5	22
6	25
7	28
8	32
9	35
10	38
11	40
12	42

Figure 4.3. Concentration of urinary C-peptide (corrected by creatinine) during the first 12 months postpartum.

Months from 1st postpartum menses	Long LA period (ng/mg creatinine)	Intermed LA period (ng/mg creatinine)	Short LA period (ng/mg creatinine)
-6	15	15	15
-5	15	15	15
-4	15	15	15
-3	15	15	15
-2	15	15	15
-1	15	15	15
0	15	15	15
1	15	15	15
2	15	15	15
3	15	15	15

Figure 4.4. Mean concentration of urinary C-peptide (corrected by creatinine) aligned by date of first postpartum menstruation in women with relatively short (3–6 mo,  $n = 15$ ), average (6–12 mo,  $n = 39$ ), and long periods of lactational amenorrhea (12–18 mo,  $n = 16$ ).



may reflect temporary insulin resistance among women with longer durations of amenorrhea, perhaps related to higher levels of prolactin (Bauman et al. 1982; Flint 1985; McNamara 1995). By combining an analysis of physiological markers of energy metabolism with indices of reproductive axis activity and behavioral observations of nursing behavior we hope to be in a position to evaluate the nursing intensity hypothesis and relative metabolic load hypothesis in the Toba context.

In sum, lactating women in Namqom represent one of the rarely reported cases of high nutritional status/intensive nursing populations that could serve to distinguish the intensity of nursing from the metabolic load hypothesis. For well-nourished Toba women, the metabolic cost of lactation represents less of a load than for women with low energy availability. Regardless of the intensity of the nursing pattern, these women can afford (in terms of energy) to shorten the period between lactation and the next gestation. Their physiology is responding to a local ecological context that allows them to meet (and even surpass) the energy requirements of lactation, gestation, and survival. Despite a nursing frequency nearly as high as that of the !Kung, they achieve fertility rates almost as high as those of the Hutterites (Eaton and Mayer 1953). Further analysis of energy metabolism in relation to the resumption of ovarian function, will provide insights into the mechanisms of fecundity regulation.

### CONCLUSION

The proximate causes of the contraceptive effect of lactation are still a matter of productive debate. Although the metabolic load hypothesis is gaining increasing empirical support, the original appeal of the nursing intensity hypothesis seems to persist. Unfortunately, when two competing hypotheses get about equal support, they tend to be polarized. It should be stressed that the metabolic load hypothesis does not negate the importance of the suckling stimulus. Both hypotheses agree that lactation is the major determinant of the period of postpartum infecundity. In fact, when the breastfeeding woman's energetic budget is limited (for example, under malnutrition or under high energetic output), the intensity of lactation can be taken as a proxy for the relative cost of lactation for that woman.

From an evolutionary perspective, both hypotheses would agree that natural selection seems to have favored a mechanism (via lactation) to reduce the probability of dangerously close births. The nursing intensity hypothesis, as mentioned before, argues that in our formative past, infants had continuous access to the breast and breast-fed on demand day and night. The high frequency with which a young, unsupplemented baby would suckle would be the signal for suppressing the mother's reproduc-

tive system. As the baby becomes older, nursing frequency declines, which allows optimum birth intervals. The problem with this argument is that it rests on the assumption that there is no constraint on the feeding schedule of the infant. Populations differ widely in both the physical and the social environment in which lactation occurs. As a consequence, we find an enormous variation in nursing behavior depending on work schedules, presence of other children, social pressure to breast-feed or not, and individual maternal temperament. Temporal nursing patterns, then, may be a poor signal for the optimal resumption of postpartum fecundity. Not only might nursing intensity not be a simple reflection of infant demand, it would not reflect the relative burden on the mother of meeting that demand.

In contrast, a mechanism that relied on monitoring the energy available to the woman for resuming postpartum fecundity would make much more evolutionary sense. This mechanism would help to regulate the female's reproductive effort in the long term as well as the short term. We assume that natural selection would favor mechanisms that optimize the allocation of energy in reproductive effort. Given the costs of pregnancy and lactation, and for the many reasons iterated above, a female should not attempt to conceive again if her energy balance is poor. On the other hand, when her energy balance becomes positive, another reproductive attempt becomes feasible.

There is no longer any doubt that lactation exerts a powerful suppressing effect on postpartum fecundity and, consequently, on fertility in non-contracepting populations. A better understanding of the regulation of postpartum fecundity will come with further research into the interface between energy metabolism and reproductive physiology.

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### NOTE

1. Maternal condition is here taken as an umbrella term that reflects the energy available to the mother and generally involves such measures as maternal energy balance and nutritional status.

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