

# ENERGY METABOLISM AND THE EVOLUTION OF REPRODUCTIVE SUPPRESSION IN THE HUMAN FEMALE

Grazyna Jasienska

Department of Anthropology, Harvard University, Cambridge, USA and Institute of Public Health, Jagiellonian University, Kraków, Poland.

Correspondence: Dr Grazyna Jasienska, Institute of Public Health, Jagiellonian University, Grzegórzecka 20, 31-351 Kraków, Poland. Tel.: (48-12) 421-62-18. Fax: (48-12) 421-74-47. Email: jasienska@post.harvard.edu

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## ABSTRACT

Reproduction places severe demands on the energy metabolism in human females. When physical work entails higher energy expenditure, not enough energy will be left for the support of the reproductive processes and temporal suppression of the reproductive function is expected. While energy needed for reproduction may be obtained by increases in energy intake, utilization of fat reserves, or reallocation of energy from basal metabolism, several environmental or physiological constraints render such solutions unlikely. For human ancestors increases in energy intake were limited by availability of food, by labor of food preparation and by metabolic ceilings to energy assimilation. Energy stored as fat may support only a fraction of the requirements for reproduction (especially lactation). Effects of intense physical activity on basal metabolism may also interfere with fat accumulation during pregnancy. Finally, the female physiology may experience demands on increasing the basal metabolism as a consequence of physical activity and, at the same time, on decreasing the basal metabolism, when energy to support the ongoing pregnancy or lactation is inadequate. The resulting metabolic dilemmas could constitute a plausible cause for the occurrence of reproductive suppression in response to physical activity. It is, therefore, likely that allocating enough energy to the reproductive processes during periods when energy expenditure rises may be difficult due to physiological and bioenergetic constraints. Females attempting pregnancy in such conditions may compromise their lifetime reproductive output. A reproductive suppression occurring in low energy availability situations may thus represent an adaptive rather than a pathological response.

**Keywords:** energy allocation; energy budget; physical activity; ovarian function; cancer prevention.

## 1. INTRODUCTION

The situations in which inadequate caloric intake and high energy expenditure resulted in an insufficient amount of energy for an individual are common throughout the course of human evolution (Leonard and Robertson, 1997). Therefore, adaptive



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physiological responses to temporal shortages of energy are expected in humans (Hoyenga and Hoyenga, 1982). This paper focuses on a short-term suppression of the reproductive function in females as an example of such a response. The suppression prevents females from investing in a reproductive event which has a low probability of success. In addition, reproductive suppression allows for the repair of maternal nutritional status, between one child and the next, possibly increasing lifetime fertility (Ellison, 1990).

This paper is an attempt to present an explanation for the phenomenon of reproductive suppression from an evolutionary perspective, i.e. "Why has such a response evolved?". It is, therefore, not aimed at adopting a mechanistic, physiological perspective ("How does it work?"), i.e. reviewing biochemical and physiological mechanisms which underlie suppression of the reproductive function. Instead, the main goal of this paper is to review physiological and bioenergetic constraints which in some situations may prevent a female from allocating enough energy to reproductive processes. Such constraints reflect the functional integration of the organism in which the needs of maintaining various processes may be in conflict with each other when they all draw from the same pool of energy or nutrients (Townsend and Calow, 1981). Special attention will be given to scenarios in which reproductive suppression results from increases in energy expenditure, in particular when an individual female is forced by ecological conditions to experience a heavy workload.

Reproductive suppression is understood as any change in the reproductive function which lowers the probability of pregnancy. Reproductive suppression resulting from environmental stress occurs in women in gradual fashion (Prior, 1985; Ellison, 1990). A small reduction in energy intake may cause low progesterone production in the luteal phase of the menstrual cycle, which lowers the probability of implantation. A more serious energy limitation may result in the lack of ovulation, and an even lower intake - in total suppression of cycling (amenorrhea). It is clear that the probability of pregnancy is reduced to zero when menstrual cycles are anovulatory or absent. However, it should be stressed that even when cycles are ovulatory, but are characterized by reduced levels of ovarian steroid hormones (progesterone and estradiol), the chances of conception, of implantation of the embryo, or of maintaining the ongoing pregnancy may be diminished (Eissa *et al.*, 1986; McNeely and Soules, 1988; Dickey *et al.*, 1993).

An assumption is made that the observed physiological responses of the reproductive system of contemporary women are not pathologies, but reflect important features of human biology during the evolution of modern humans (e.g. the period before the introduction of agriculture, and more specifically the late Paleolithic era). Human physiology has remained basically unchanged since that time (Eaton *et al.*, 1988) and energetic stresses are still salient features of life in many traditional populations (Roberts *et al.*, 1982; Lawrence and Whitehead, 1988; Panter-Brick, 1993; Adams, 1995; Benefice *et al.*, 1996; Sellen, 2000). Consequently, understanding reproductive responses to caloric restrictions and increases in levels of energy expenditure has relevance ranging from evolutionary biology and demography of *Homo sapiens* to practical medical applications (Booth *et al.*, 2002). There is, for example, growing epidemiological data on reduction in breast cancer risk in women as a result of recurring reproductive suppression caused by energetic factors (Friedenreich *et al.*, 1998; Bernstein, 2002). Recently, energetic factors have also been

discussed in relation to reproductive physiology of human males (Bribiescas, 2001) and non-human primates (Knott, 2001).

Energy-related reproductive suppression can result either from reduction in energy intake or from increases in energy expenditure. Either factor can cause changes in energy allocation and often lead to a negative energy balance. It is important to note however, that an increase in the level of physical activity, even when not causing negative energy balance, may still result in reproductive suppression. In women who increase their levels of energy expenditure, sufficient energy for reproduction could theoretically be obtained by increases in energy intake, utilization of fat reserves, or reallocation energy from basal metabolism. The main point of this paper is that such solutions may often be unavailable, due to environmental or physiological constraints. I outline the state of knowledge about the energetics of reproduction in women and then review two hypotheses from evolutionary physiology aimed at explaining why reproductive suppression occurs under energetic limitations (Jasienska and Ellison, 1998; Jasienska, 2001). The hypotheses are not mutually exclusive and concern different metabolic constraints that a reproducing female is forced to confront.

The first hypothesis addresses the existence of limits on increasing the energy intake. Theoretically, an increase in energy expenditure can be matched by a similar increase in energy intake. If such a situation occurs, a woman may still have enough energy to support both intense physical activity and the demands of pregnancy and lactation. During the evolutionary past of *Homo sapiens*, a significant increase in energy intake was probably difficult to obtain. First of all, in hunting-gathering Paleolithic societies searching for additional food and labour intensity of food preparation (O'Dea, 1991) were, most likely, associated with an even higher increase in the levels of energy expenditure. More importantly, even when enough food was available, the assimilation of additional energy was limited by physiological constraints, e.g. metabolic ceilings to energy assimilation.

The second hypothesis is based on the assumption that an increase in physical activity may interfere with energy-saving mechanisms normally available to a reproducing female. In individuals experiencing intense physical effort, the basal metabolic rate (BMR, the fraction of energy which is used to support the maintenance metabolism) rises. An increase in the BMR creates a dilemma in the physiology of pregnant and lactating women in situations when reduced availability of energy would force them to adopt energy-saving strategies. The dilemma arises since one of these strategies would be a reduction in the BMR, resulting from the re-allocation of energy from the female's physiological needs to the energetic demands of pregnancy and lactation. Intense physical activity may therefore restrict the ability to obtain energy savings from BMR reduction. In such a situation, a woman with inadequate energy intake may not be able to store fat during pregnancy. Without sufficient fat reserves and a compromised ability to lower BMR also during lactation, her lactational performance may suffer. In addition, although the energy reserves in the form of fat storage are in human females more substantial than those in many other mammals, they are still insufficient to support a single reproductive event (e.g. full pregnancy and lactation).

## 2. ENERGETIC COSTS OF REPRODUCTION

Reproduction in the human female requires energy to maintain ovarian and uterine function, and especially to support pregnancy and lactation. The maintenance of menstrual cycles is not energetically expensive: during several days of the luteal phase of the cycle an increase of 6% to 12% in resting metabolic rate had been reported (Bisdee *et al.*, 1989; Meijer *et al.*, 1992; Howe *et al.*, 1993; Curtis *et al.*, 1996). In addition, women tend to increase their caloric intake during the days following ovulation (Johnson *et al.*, 1994). That evidence points to the fact that some additional energy beyond the regular metabolic needs is required to support regular menstrual function (Strassmann, 1996). However, not the costs associated with menstrual cycles, but much higher and longer lasting energetic demands of pregnancy and lactation are the ultimate factors behind the phenomenon of reproductive suppression.

For well-nourished women from industrialized countries the estimated costs of pregnancy constitute an expense of, on average, an extra 1000 - 1250 kJ a day (Hyttén and Leitch, 1971; Durnin, 1991; Dewey, 1997). During the last trimester of the pregnancy a woman may require up to 22% of additional energy over the pre-pregnant values (Hyttén and Leitch, 1971; Butte *et al.*, 1999). Energetic costs of lactation are even higher. They change with the age of the infant (Rashid and Ulijaszek, 1999) and the frequency of feeding, but, on average, lactation requires additional 2000 kJ/day (van Raaij *et al.*, 1991; Dewey, 1997) and may last a few years. It should be pointed out that recently these estimated costs were criticized as being too high in comparison to the actual energetic intakes of pregnant and lactating women from non-industrial populations (Illingworth *et al.*, 1986; Kopp-Hoolihan *et al.*, 1999). Well-nourished British women had the average energy intake of 8300 kJ/day when pregnant, and over 9500 kJ/day while lactating (Prentice, 1984). In Swedish women the total energy requirements of lactation were 12000 kJ/day during the exclusive breastfeeding period at three months postpartum (Butte *et al.*, 2001). In comparison, rural Gambian women during the wet (hunger) season supported pregnancy and lactation on the average energy intake of only 5400 kJ/day (Prentice, 1984).

It should be stressed that women are capable of supporting reproduction on a limited energy supply, but such a strategy entails substantial long-term costs. Reproduction in women in poor energetic condition is associated with diminished reproductive outcome, reflected both in the health condition of the newborn child (Lechtig *et al.*, 1975; Roberts *et al.*, 1982; Lawrence *et al.*, 1987a; Kusin *et al.*, 1992; Siniarska *et al.*, 1992; Pike, 2000) as well as in a further decline of nutritional status of the mother ("the maternal depletion syndrome") (Liu *et al.*, 1988; Merchant and Martorell, 1988; National Academy of Sciences Committee on Population, 1989; Tracer, 1991; Little *et al.*, 1992; Miller *et al.*, 1994; Khan *et al.*, 1998; Winkvist *et al.*, 1998; Pike, 1999; George *et al.*, 2000), which may, in turn, negatively affect her future reproductive potential.

## 3. REPRODUCTIVE SUPPRESSION CAUSED BY ENERGY EXPENDITURE

Reproductive suppression resulting from intense physical activity has been described both in women from industrial countries participating in professional and recreational sports (Ellison, 1990; Rosetta, 1993; De Cree, 1998; Rosetta *et al.*, 1998;

Arena and Maffulli, 2002) and in women from traditional societies engaged in work-related activities (Ellison *et al.*, 1989; Bailey *et al.*, 1992; Panter-Brick *et al.*, 1993; Jasienska and Ellison, 1998).

Intense sport training in ballet dancers, rowers, marathon runners, swimmers and gymnasts, may cause severe disturbances of menstrual function, e. g. often total lack of or infrequent cycles (Dale *et al.*, 1979; Frisch *et al.*, 1980; Warren, 1980; Schwartz *et al.*, 1981; Veldhuis *et al.*, 1985; Cumming, 1993; Zanker and Swaine, 1998). Interestingly, even moderate levels of recreational physical activity in untrained women may have suppressive effects on reproductive function (Ellison *et al.*, 1987; Hoshi *et al.*, 1989; Broocks *et al.*, 1990; De Souza *et al.*, 1998; Williams *et al.*, 1999). These women often have cycles of regular duration, but show low levels of ovarian steroid hormones, disturbed follicular development and shortened luteal phases (Ellison *et al.*, 1987; Hoshi *et al.*, 1989; Broocks *et al.*, 1990; De Souza *et al.*, 1998).

Sport and work-related physical activity often lead to weight loss, which indicates a negative energy balance. However, in some studies the participating women did not lose weight (i.e. had neutral energy balance) (Bullen *et al.*, 1985; Ellison and Lager, 1986; Jasienska and Ellison, 1993, 1998; Jasienska, 1996), but still experienced reproductive suppression, as determined by the lowered levels of ovarian hormones. These results show that physical activity by itself, independently of negative energy balance, may suppress ovarian function in women.

Women involved in subsistence work show seasonal changes in ovarian function following changes in food availability and work demands. Lese women who lost weight during the hunger season had lower progesterone levels and ovulatory frequency than women from the same community who did not experience weight loss. After the hunger season, increases in progesterone levels and ovulatory frequency were observed in all women, in parallel to the overall improvement in the nutritional status (Ellison *et al.*, 1989; Bailey *et al.*, 1992). Seasonal ovarian suppression had a significant influence on fertility, as reflected by both seasonality and inter-annual variation of births. The lowest conception rate was observed during years with particularly severe hunger seasons (Bailey *et al.*, 1992), showing that successful pregnancy had less chance to occur during times of low energy availability. Similarly, introduction of modern technology which led to a decline in energy expenditure, lowered the age of first reproduction in rural Maya women (Kramer and McMillan, 1999) and reduced length of first birth intervals in rural Ethiopia (Gibson and Mace 2002). In Nepal, the Tamang women experienced seasonal increases in work intensity and related changes in energy balance. Ovarian function was suppressed in women who lost weight during the period of intense physical work (Panter-Brick *et al.*, 1993; Panter-Brick and Ellison, 1994).

In both Lese and Tamang populations, the effects of intense physical activity on the reproductive function are confounded with the effects of negative changes in energy balance. While Lese women experience severe food shortages, even in Tamang women the nutritional status is likely to play a role in the ovarian suppression. Although energy intake was quite constant across the year in this Nepali population, 22% of the women studied still had the body mass index of less than 18.5 kg/m<sup>2</sup> indicating chronic energy deficiency (Panter-Brick, 1996).

In contrast to the previously described results, the Polish women-farmers did not lose weight or body fat (which indicated neutral energy budget) during the season of

intense harvest-related work (Jasienska and Ellison, 1998). As indicated by the levels of ovarian progesterone, they experience significant suppression of ovarian function during that time of the year. In addition, as shown by path analyses, the mean total daily energy expenditure was the only factor responsible for the suppressed levels of ovarian progesterone. Body weight, body fat percentage, or changes in these nutritional indices showed no relationships with the levels of the ovarian steroids (Jasienska and Ellison, 1998).

#### 4. ENERGY INTAKE AND METABOLIC CEILINGS TO ENERGY ASSIMILATION

Recent studies show in many species the existence of physiological limits to the rate of food conversion into usable energy (Saris *et al.*, 1989; Peterson *et al.*, 1990; Weiner, 1992; Hammond *et al.*, 1994; Konarzewski and Diamond, 1994; Hammond *et al.*, 1996; Suarez, 1996; Hammond and Diamond, 1997). When an individual is experiencing high energetic demands, increases in the food intake, at some point, cease to generate additional energy. In fact, in all the studied species (including birds, eutherian mammals and marsupials) only metabolic rates not higher than just several times the BMR could be supported entirely by the energy intake, without depleting energy reserves (Peterson *et al.*, 1990; Hammond and Diamond, 1997). Metabolism completely fueled by energy intake is called the sustained metabolism (Peterson *et al.*, 1990). Regardless of the species studied, the ratio of sustained to basal metabolic rate (SusMR/BMR) was always reported to be below seven (Peterson *et al.*, 1990).

Sustainable energy budgets appear to be limited by the maximum rate of energy assimilation (Weiner, 1989; Hammond *et al.*, 1994). The maximum rate of energy assimilation is, in turn, constrained by either the capacity to digest food or by the capacity to absorb nutrients and energy (Weiner, 1992). Theoretically, since these last two functions are determined by morphology and size of the digestive track, changes in these characteristics should provide the individual with an increased ability to generate more energy from a unit of food. Such modifications of the digestive track are known to occur as a result of seasonal changes in the requirements for energy or seasonal changes in food quality (Weiner, 1992). The changes are usually not permanent, however. Their reversibility implies that there are substantial energetic costs associated with increasing and maintaining the gut of larger size (Weiner, 1992).

Several studies investigated limits to sustainable energy budgets in modern human males, reporting values for SusMR/BMR between 4.1-5.6 (Saris *et al.*, 1989; Peterson *et al.*, 1990). Tour de France cyclists during the 22 day-long race had the estimated total daily energy intake of 24,700 kJ and mean total daily energy expenditure of 25,400 kJ, which is probably the highest level of prolonged energy expenditure ever reported for humans (Saris *et al.*, 1989). In comparison, male army soldiers expend between 13,500 to 21,000 kJ a day, and Antarctic explorers from 18,500 to 23,000 kJ a day (Peterson *et al.*, 1990). The Tour de France cyclists probably reach the upper limits to sustainable energy budgets, e.g. they would not be able to generate more energy with additional increase in food consumption (Peterson *et al.*, 1990).

Are physiological limits to energy budgets just a modern phenomenon resulting from extreme and “unnatural” intensity of sport activities? Or, were these limits also present throughout the course of human evolutionary history serving as constraints on

the amounts of energy obtained from food and on patterns of energy allocation? The sustainable energy budgets exhibited by the Tour de France cyclists obviously represent a physiological extreme. It is unlikely that such high levels of energy intakes and expenditures were ever experienced by human ancestors, especially women (Leonard and Robertson, 1997). However, the issue to consider here is the change in food quality from that typical for hunting and gathering ancestral societies to that of modern industrial populations (Southgate, 1991; Ulijaszek, 1991). Although there probably was a considerable variation in the diet of the Paleolithic *Homo sapiens* (Eaton *et al.*, 1988), it is clear that food was characterized then by the higher percentage of fibre, lower fat and lower simple carbohydrates than the modern industrial diets (Cordain *et al.*, 2000). The consumption of dietary fibre in several contemporary hunter-gatherer populations is about 100 grams a day, while in North Americans, by comparison it averages about 15 grams a day (Eaton *et al.*, 1994). Among the !Kung San, who are frequently used as the model of the human ancestral lifestyle, 60 to 80% of the consumed energy is provided by plant food (Lee, 1979). Such diets, like that of modern Australian Aboriginal hunter-gatherers are characterized by low energy density (O'Dea, 1991). In fact the only carbohydrate source with high energy density in traditional diets was wild honey (O'Dea, 1991). The carbohydrates found in many traditional diets were shown to be more slowly digested and absorbed than the equivalent carbohydrates from domesticated plants (Thorburn *et al.*, 1987).

It is possible that high SusMR/BMR ratios observed in modern athletes are permitted by the excellent quality of their diet (Westerterp, 2001), in particular the high energy density. Modern athletes have high levels of energy expenditure but also a very high quality diet. Paleolithic humans had lower levels of energy expenditure, but also a much lower diet quality. Therefore, it can be hypothesized that in our ancestors metabolic ceilings to energy budgets were also relevant, but they had much lower values than in modern athletes. If that was the case, then in the evolutionary past an increase in energy expenditure might have been compensated by an increase in energy intake, but only to a certain extent. Even when the availability of food was sufficient, the maximum rate of energy assimilation acted as the main factor limiting the sustainable energy budgets. Any increase in energy expenditure was therefore likely to result in an inadequate energy remaining for support of reproductive processes. An ability to temporally suppress reproductive function had in such circumstances a clear adaptive significance.

## 5. THE BMR DILEMMA

Both long-term increases and reductions in the basal metabolic rate have been observed. An elevation of the BMR can be caused by an increase in physical activity, especially when the resulting enlargement in the energetically expensive muscle tissue imposes higher energetic demands. On the other hand, a reduction in the BMR is a crucial energy-saving strategy for women in poor energetic status supporting pregnancy or lactation. Therefore, there are demands on increasing the BMR due to higher physical activity and on decreasing the BMR, when energy to support the ongoing pregnancy or lactation is insufficient.

*The increase of basal metabolism due to physical activity*

Many studies reported an increase in the BMR as a result of prolonged sport participation (Poehlman and Horton, 1989; Van Zant, 1992; Burke *et al.*, 1993; Sjodin *et al.*, 1996; Tremblay *et al.*, 1997; Dolezal and Potteiger, 1998; Morio *et al.*, 1998). It should be noted however, that this effect was not always confirmed. There is also data on the existence of a short-term increase in the BMR immediately after exercise (Bingham *et al.*, 1989) or a decrease in the BMR due to chronic exercise (Westerterp *et al.*, 1994). Increases in the BMR should, in general, be expected in individuals who have experienced changes in body composition, especially when longer-term physical training have led to the increases in muscle mass. The muscle, as a metabolically active tissue, is energetically expensive to support (McArdle *et al.*, 1986). When a training regime does not produce changes in body composition, a change in the BMR is unlikely to occur. For example, both low and high-intensity 15-week resistance training failed to cause significant changes in the body composition in women (Taaffe *et al.*, 1995). Not surprisingly, the BMR of these women remained at the pre-exercise level. In contrast to the last finding, both the studies of endurance athletes (who usually have a higher percentage of fat-free mass than less athletic people) and the studies during which the training caused changes in body composition often report positive effects of training on the BMR. In women rowers changes in the BMR reflected changes in fat-free mass (McCargar *et al.*, 1993). The BMR of elite endurance athletes was 16% higher than in the non-athletic control group (Sjodin *et al.*, 1996). Significant increases in the BMR after 10 weeks of training were reported in males engaged in resistance training, but not in males participating in endurance training (running and/or jogging) (Dolezal and Potteiger, 1998), possibly reflecting differences in the muscle mass gain.

Interestingly, not only physical activity but also the rate of energy flow (i.e. both high energy intake and high energy expenditure) are positively correlated with the resting metabolic rate (RMR) (Burke *et al.*, 1993; Bullough *et al.*, 1995). The RMR rose only in the trained men characterized by a high rate of energy flow (Bullough *et al.*, 1995). Also in women the RMR showed a positive relationship with energy flow and aerobic fitness (determined by  $VO_{2\max}$ ) (Burke *et al.*, 1993). A long-term physical activity, especially when associated with changes in body composition and high rates of energy flow, may thus induce significant increases in the basal metabolism.

*The reduction of basal metabolism during pregnancy and lactation*

In humans, both pregnancy and lactation are energetically expensive. Costs of pregnancy result from fetal growth, growth and maintenance of maternal supporting tissues, and maternal fat accumulation (Hyttén and Chamberlain, 1991; Blackburn and Loper, 1992). Energetic demands of lactation are a consequence of milk synthesis and the maintenance of metabolically active mammary glands (Trayhurn, 1989; Prentice and Prentice, 1990; Lunn, 1994). Since the BMR is the index integrating all metabolic activities, it is expected to rise in women who are pregnant or nursing a child. However, when the environmental conditions do not provide adequate energy, the physiology of women who are already pregnant or lactating may be forced to rely on energy saving strategies in order to support energetic demands of the child (Peacock, 1991).



One mechanism which allows for reallocating more energy to reproduction is a reduction in the maternal basal metabolism (Prentice *et al.*, 1989; Peacock, 1991; Prentice *et al.*, 1995). Such a reduction indicates that some of the metabolic processes (e.g. some components of the maintenance metabolism, like protein turnover) are temporarily slowed down or even halted (Prentice and Whitehead, 1987; King *et al.*, 1994). However, a long-term reduction in the BMR is not neutral and may be even detrimental to the maternal health.

The BMR of a pregnant woman should increase during each of the four quarters of pregnancy respectively by about 3, 7, 11 and, 17% above pre-pregnant values (Hyttén and Leitch, 1971). Empirical data usually support the theoretical predictions only in women in a good energetic status (Prentice and Whitehead, 1987; Prentice *et al.*, 1989; Prentice and Prentice, 1990; Durnin, 1991; Durnin, 1993; Lunn, 1994; Prentice *et al.*, 1995; Prentice *et al.*, 1996; Butte *et al.*, 1999): in Swedish women BMR increased from the very beginning of the pregnancy (Prentice and Whitehead, 1987). However, in women from Scotland and Gambia, in poorer nutritional condition, BMR showed a significant decrease up to the 12th week of pregnancy. The BMR of these women approached the pre-pregnant values as late as the 22-26 week, and started to rise further, but even at delivery it was still much lower than the BMR of Swedish women (Prentice and Whitehead, 1987). Pregnant Nigerian women showed significant variability in BMR, which corresponded to variability in their nutritional status (Cole *et al.*, 1989). Even well-nourished Western women show significant variation in the BMR responses to pregnancy paralleling differences in pre-pregnant body fat (Prentice *et al.*, 1989). During pregnancy maternal adipose reserves serve as a highly significant predictor of changes in BMR (Bronstein *et al.*, 1996). Reduction in the BMR at the beginning of pregnancy is therefore of crucial importance for women in poor nutritional condition. Lowering the BMR not only considerably reduces energetic costs of pregnancy, but also allows women to allocate some energy into fat storage which may be invaluable for the support of lactation.

Lactation is predicted to cause, on average, a 12% increase in BMR above the non-pregnant values (Hyttén and Leitch, 1971). The BMR does not always increase according to theoretical predictions. During lactation, the BMR has been observed to increase, decrease or remain at pre-pregnant levels (Lawrence and Whitehead, 1988; Goldberg *et al.*, 1991; Forsum *et al.*, 1992; Guillermo-Tuazon *et al.*, 1992; Madhavapeddi and Rao, 1992; Piers *et al.*, 1995). Variation in the BMR responses here can also be explained by differences in the nutritional status of the women studied (Prentice and Prentice, 1990). Women from Gambia during the first year of lactation showed a 5% decrease in the BMR compared to the pre-pregnant values (Lawrence and Whitehead, 1988). This small reduction in BMR saves about 500 kJ a day and, in comparison to women who increased their BMR during lactation, savings add to about 900 kJ a day. The saved energy can be allocated into synthesis of milk and help mothers with low energy intake to support a child. The savings from the reduction of BMR, although not sufficient to cover the whole expense of breast-feeding, are still significant, since average daily cost of milk production for the Third World women is about 2000 kJ (Lunn, 1994).

Reproduction in women who are in a poor nutritional status is characterized by marked decreases of BMR during pregnancy and lactation. The BMR reduction is important as an energy saving mechanism, especially in women who are not able to

sufficiently increase their food intake while pregnant or lactating. However, since intense physical activity forces the rise in the BMR, the organism of a hard-working and pregnant or lactating woman may have a restricted ability to lower the BMR. At the same time if the physical activity restricts the ability to obtain energy savings from reducing the BMR, storing fat at the beginning of pregnancy is also compromised. Without sufficient fat reserves and without the ability to lower the BMR also during lactation, the lactational performance of the women may suffer. In the situation of a deterioration of environmental conditions this lactating woman will not be able to generate sufficient energy to support milk production. Therefore, since the BMR reduction is not available as an energy-saving option in hard-working women, reproductive suppression occurs.

## 6. THE INSUFFICIENCY OF FAT RESERVES

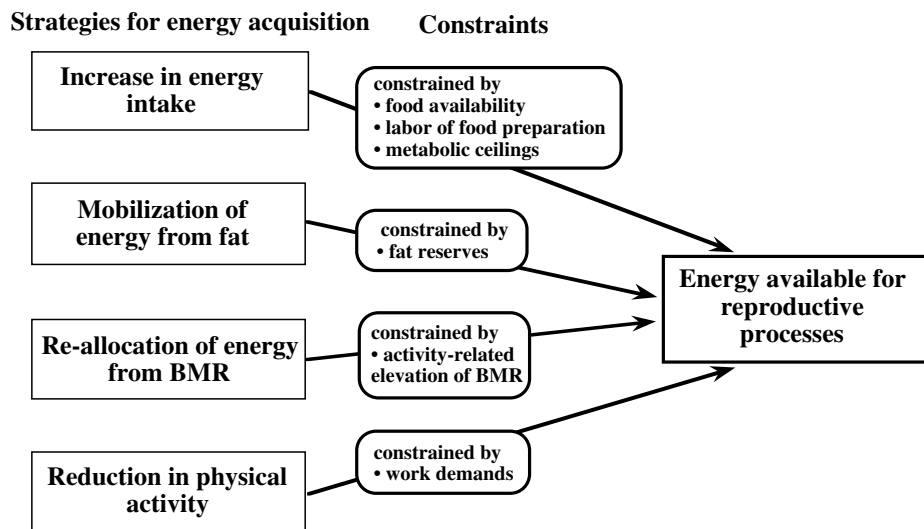
It has been suggested that energetic reserves in the form of stored fat are for human females of importance in the context of reproduction (Frisch, 1990; Vernon and Pond, 1997). Fat stores may indeed be crucial for partially covering the energetic costs of milk production (McNamara, 1995). The data showing that women in developing countries often have very low fat reserves (Lawrence *et al.*, 1987b; Little *et al.*, 1992; Panter-Brick, 1996) led to the hypothesis that in the developing world the function of fat stores is to serve as an emergency resource for times when conditions become very hard, rather than to steadily support milk production (Prentice and Prentice, 1990; Lunn, 1994). If fat reserves were to be used to subsidize just 50% of the costs of lactation they would last for only four months in Gambian women (Prentice and Prentice, 1990). In contrast, the fat stores would last for 11 months when used to support half of lactation costs in well-nourished Western women.

## 7. CONCLUSIONS

It is likely that in the evolutionary past of our species, high levels of physical activity usually resulted in reproductive suppression in females. The two seemingly most obvious solutions (i.e. eating more or doing less) of obtaining enough energy for reproduction were probably simply unavailable for our ancestors, just as they are today for many women in hunting and gathering or agricultural populations (Panter-Brick, 1993; King *et al.*, 1994; Jenike, 1996; Prentice *et al.*, 1996; but see also Bentley *et al.*, 1999). Energy intake was constrained not only by the availability of food but also by metabolic ceilings to energy assimilation. This issue may be worth considering even though the ideas on the importance of metabolic ceilings in human evolutionary history are speculative and have so far been supported only by studies on extreme levels of physical activity. Nevertheless, it is clear that there are considerable dietary differences between ancestral and modern humans, which may result in different levels of metabolic ceilings. The ceilings of the past, related to diets of lower energy density, were probably much lower.

On the other hand, the patterns of energy allocation to all energy demanding functions had some degree of flexibility, allowing for the prevention of reproductive failure in pregnant and lactating females when environmental conditions had deteriorated (Figure 1). Such flexibility however, might have been substantially diminished in females who were simultaneously under pressure to sustain high levels

of physical activity. Therefore, high energy expenditure resulting from intense workloads might have been used as a signal that not only not enough energy would be available for reproduction, but also that it would be impossible to use the energy-saving mechanisms during pregnancy and lactation. Consequently, when physical activity increases energetic demands and interferes with energy-saving mechanisms, the temporal suppression of reproductive function may be expected. Such reproductive suppression could then be treated as an evolved response, ensuring the survival of the female and the maintenance of her future reproductive potential.



**Figure 1.** Constraints on the allocation of additional energy to reproduction may result in inadequate energy to support the reproductive processes. Low energy availability may cause reproductive suppression in individuals experiencing demands for intense physical activity.

The concept of the metabolic dilemma resulting from responses of BMR in different situations needs empirical verification. It would be interesting to determine if women who increase their levels of physical activity, and therefore their BMR during pregnancy, will have diminished abilities to store fat. Further, I propose that the ability to store fat will be even lower in women who are in poor energetic condition as a result of physical activity, compared to women who are in poor energetic condition due to caloric restriction alone.

Sport participation has been the only factor shown so far to influence the BMR levels in humans. In order to use evidence from BMR research to make an evolutionary argument for the existence of reproductive suppression it needs to be shown that a similar effect on basal metabolism may also be exerted by occupational, physical work. Similarly, the existence of metabolic ceilings to energy budgets awaits a study in non-industrial populations. Such studies have potential relevance also for the area of general nutrition and human health management.

Recently, a growing number of studies in cancer (especially breast cancer) prevention research have documented the protective effect of lifetime physical activity

on cancer risk (Friedenreich *et al.*, 1998). The existence of such a protective effect is beyond contention. The mechanism is unknown, but it is hypothesized that the beneficial effect of physical activity is due to the reduced levels of steroid hormones, resulting in reproductive suppression in pre-menopausal women (Pike *et al.*, 1993; Jasienska and Thune, 2001a, 2001b). However, the majority of studies in cancer epidemiology point to a negative energy balance of the individual as that aspect of physical activity which brings about a lowered cancer risk. In contrast, the arguments presented in this paper stress that negative energy balance is not a *sine qua non* condition for the occurrence of reproductive suppression in physically active women (Jasienska *et al.*, 2000). Remarkably, even the changes in patterns of energy allocation imposed by physical activity may be sufficient for reproductive suppression to occur. The understanding of such a scenario may be important in preventive medicine when designing cancer protection programs for women.

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