AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 131:295–302 (2006)

Changes in Body Fat Distribution in Relation to Parity in American Women: A Covert Form of Maternal Depletion

William D. Lassek* and Steven J.C. Gaulin

Department of Anthropology, University of California at Santa Barbara, Santa Barbara, California 93106-3210

KEY WORDS fat metabolism; pregnancy; lactation; brain development

ABSTRACT Using data from the Third National Health and Nutrition Examination Survey (NHANES III), conducted from 1988–1994, we investigated the effect of reproduction on the distribution of body fat in well-nourished American women. While women tend to gain weight and fat with succeeding pregnancies, if age and body mass index are controlled, increasing parity is associated with a decrease in hip and thigh circumferences, suprailiac and thigh skinfolds, and body fat estimated from skinfolds, while waist circumference increases, resulting in a relative decrease in lower-body fat. The mobilization of fat stores in the lower body during late pregnancy and lactation may help to meet the special needs of the developing brain for essential fatty acids and energy during the time of peak growth. When fat is regained after the postpartum period, relatively more is stored in central vs. peripheral depots, resulting in a patterned change in body shape with parity. Am J Phys Anthropol 131:295–302, 2006. ©2006 Wiley-Liss, Inc.

One striking difference between humans and other primates is the extensive fat store in human females. During childhood and puberty, well-nourished human females deposit 15–20 kg of fat, representing 25–30% of body weight, mainly in subcutaneous tissues of the hips and thighs (Durnin et al., 1987; van Raaij et al., 1989; Koop-Hoolihan et al., 1999; Forsum et al., 1988), while males store much less. In a recent Dutch study, young postpubertal women averaged 15.3 kg of body fat (27%), compared with 5.3 kg (8%) for males (Boot et al., 1997).

This difference in fat storage produces sexually dimorphic body shapes. By contrast, nonhuman primates in the wild have low body fat and little dimorphism in shape (Pond, 1997). Fat stored in the hips and thighs appears to be protected from mobilization until late pregnancy and lactation (Rebuffe-Scrive et al., 1985; Rebuffe-Scrive, 1987), and these fat stores tend to remain relatively constant in nulligravidas.

During the first 6 months of pregnancy, well-nourished women tend to add an additional 3.5 kg of fat to the fat stored during childhood and puberty (Hytten and Leitch, 1971; Adair and Bisgrove, 1991). This fat is also preferentially deposited in the hips and thighs (Rebuffe-Scrive, 1987), as reflected by increases in thigh and suprailiac skinfolds (Sidebottom et al., 2001; Piperata et al., 2002; Taggart et al., 1967; Forsum et al., 1989; Ehrenberg et al., 2003; Villar et al., 1992).

During the last 10–12 weeks of pregnancy, some stored fat may be mobilized to meet the needs of the growing fetus (Hytten and Leitch, 1971; Taggart et al., 1967; Adair and Pollitt, 1983; Adair et al., 1984; Forsum et al., 1989). This process continues after birth, as well-nourished lactating women tend to lose about 0.8 kg of fat per month (Prentice et al., 1992; Butte and Hopkinson, 1998; Forsum et al., 1989; Schutz et al., 1980). Previously protected fat is preferentially mobilized from the hips and thighs (Rebuffe-Scrive et al., 1985). Thigh and suprailiac skinfolds decrease (Butte and Hopkinson, 1998; Motil et al., 1998; Taggart et al., 1967), as does hip circumference (Manning-Dalton and Allen, 1983; Barbosa et al., 1997).

Women in less well-nourished populations, although smaller, still tend to have 20–25% of their body weight in fat, as in New Guinea (Jellife and Maddocks, 1964), the Gambia (Lawrence et al., 1987; Singh et al., 1989), Guatemala (Villar et al., 1992), and the Philippines (Tuazon et al., 1987), with a consistent difference between the sexes (Mueller and Reid, 1979; Eveleth and Tanner, 1990; Owa and Adejuyigbe, 1997). For example, among poorly nourished 17-year-olds in rural Kenya, females had a mean body mass index (BMI) of 18.9 and averaged 10.8 kg (23%) of fat, vs. 4.2 kg (9%) of fat in males (Kulin et al., 1982).

The fat increase in pregnancy in these populations also tends to be smaller. For example, samples of pregnant women had no increase in fat in Bangladesh (Alam et al., 2003), an increase of 0.6 kg in the Philippines (Guillermo-Tuazon et al., 1992), 1.4 kg in Thailand (Thongprasert et al., 1987), and 1.5 kg in Java (Kardjati et al., 1990). One sample in the Gambia with especially limited nutrition had a loss of 4.7 kg of fat during pregnancy (Lawrence et al., 1987).

During lactation, women in less well-nourished populations in Guatemala, Mexico, Brazil, and Taiwan, and Navajo women, also lost fat (Fornes and Dorea, 1995; Barbosa et al., 1997; Schutz et al., 1980; Butte et al., 1981; Adair et al., 1984), although the amount lost tends to be smaller. In some populations with periods of seasonal abundance and scarcity, women may even gain weight during lactation (Prentice et al., 1981).

Because of the mobilization of fat during late pregnancy and lactation, poorly nourished women may de-

*Correspondence to: William Lassek, Department of Anthropology, University of California at Santa Barbara, Santa Barbara, CA 93106-3210. E-mail: will.lassek@gmail.com

Received 20 July 2005; accepted 1 November 2005.

DOI 10.1002/ajpa.20394
Published online 4 April 2006 in Wiley InterScience (www.interscience.wiley.com).

plete fat stores accumulated during early life and become progressively thinner and lighter with each succeeding pregnancy, a phenomenon termed *maternal depletion*. This pattern was observed in New Guinea (Ventkachatalam, 1962; Jellife and Maddocks, 1964; Norgan et al., 1974; Durnin, 1980; Tracer, 1991; Garner et al., 1994), Kenya (Little et al., 1983, 1992; Shell-Duncan and Yung, 2004), Bangladesh (Huffman et al., 1985; Chowdhury, 1987; Alam et al., 2003), India (Belevady, 1979), the Philippines (Adair, 1992), Mali (Adams, 1995), Peru (Yu and Shephard, 1998), Guatemala (Merchant et al., 1990), Zaire (Pagezy, 1984), the Solomon Islands (Friedlaender and Rhoads, 1982), and Namibia (Kirchengast and Winkler, 1996).

In well-nourished women, although some fat is lost during late pregnancy and lactation, many women appear to lose less fat than they gained in early pregnancy, and thus have a net gain in fat with each succeeding pregnancy (Cederlof and Kaij, 1970; Beazley and Swinhoe, 1979; Rookus et al., 1987; Brown et al., 1992; Rossner, 1992; Keppel and Taffel, 1993; Harris et al., 1997; Wolfe et al., 1997).

If well-nourished women gain lower-body fat during the first part of pregnancy and retain some of the fat gained after the postpartum period, then we would not expect to see a change in fat distribution associated with parity, other than the addition of retained fat. However, if fat is preferentially mobilized from the lower body and fat stores from early life are affected, then we would expect to see a relative decrease in lower-body fat. The purpose of this paper is to test the hypothesis that mobilization of fat during pregnancy and lactation leads to a shift in relative fat distribution from the lower to the upper body.

METHODS

Cross-sectional data were analyzed from the Third National Health and Nutrition Examination Survey (NHANES III), conducted by the National Center for Health Statistics in 1988–1994. The sample included 16,325 females, with 4,796 from ages 0–9, 7,551 from 11–49, and 3,978 over 50. At the time of the survey, 354 were pregnant, and 103 were nursing. There were also 14,986 males with a similar age distribution. Of the females in the sample, 37.7% were non-Hispanic white, 29.3% non-Hispanic black, 28.3% Mexican-American, and 4.7% other. Because of the oversampling of blacks and Hispanics, the sample is not representative of the US population as a whole, but is representative of its largest ethnic groups. Sample weights were not used in this analysis. The disadvantages of using weights in analyses of this kind of sample were discussed by Korn and Graubard (1991). Statistical analyses were performed using SPSS.

For those under 18, the amount of body fat was estimated using the formula of Slaughter et al. (1988), based on the triceps and subscapular skinfolds. For those 18 and older, the method of Jackson et al. (1980), using triceps, suprailiac, and thigh skinfolds, was used. It should be noted that estimates of body fat based on skinfolds are less accurate during pregnancy.

RESULTS

Fat deposits over the life cycle

As found in other studies, young females in the NHANES III sample stored substantial amounts of fat during childhood and puberty, as shown in Figure 1. Based on skinfolds, by age 17, nulligravidas in this sample stored an average of 16.2 kg of fat or 25% of body weight vs. 6.3 kg (9%) in males, with a mean BMI of 23.3. From ages 10–17, females added about 1.1 kg of fat per year.

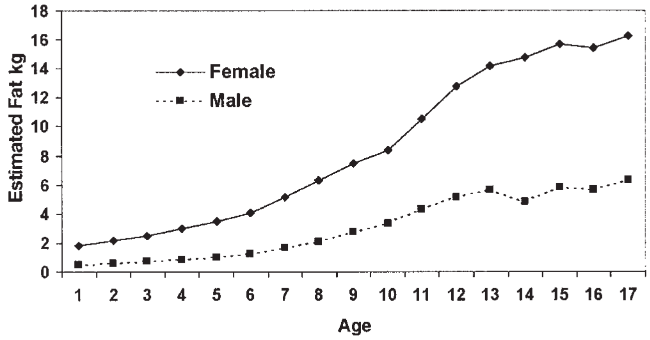

Fig. 1. Estimated body fat (kg) for males (n = 4,530) and females (n = 5,351) aged 1–17 years in NHANES III sample, based on subscapular and triceps skinfolds.

Using regression, from ages 18–34, there was no significant change in the fat mass or BMI of nulligravidas, while there was an increase of 0.35 kg in fat mass and 0.20 kg/m^2 per year in parous women ($P < 0.01$). (Over age 34, there are relatively few nulligravidas in the sample.)

Assessing the effects of reproduction on fat deposits

Because of the increase in weight and fat with age and parity, the effect of pregnancy and lactation on energy balance is difficult to see in a well-nourished population. We used four methods to try to separate the effects of pregnancy and lactation on fat distribution from those of secular weight gain.

Our first approach used multiple regression to control for the effects of increasing BMI and age by treating measures of fat distribution as dependent variables and using age, parity (measured continuously), and BMI as independent variables. The sample for this analysis includes all nulligravidas (n = 2,051) and all women who ever nursed a child (n = 1,866) for ages 11–49. The beta coefficients for parity (Table 1) indicate how much effect each live birth has on the dependent variables, separate from the effects of age and BMI. Controlling for BMI and age, each live birth *decreased* hip and thigh circumference by about 0.5 cm and the thigh skinfold by about 1 mm, with smaller decreases in the triceps and suprailiac skinfolds. Note that with the same controls, each live birth was associated with a 0.5-cm *increase* in waist circumference. These effects are small but significant.

A second way to show the effect of parity on fat distribution while controlling for increases in BMI with age and parity is to calculate the ratios of the hip, thigh, and waist circumferences to BMI. These ratios indicate the relative proportion of total body fat stored in these depots. Figure 2 shows these ratios for females aged 11–49. With increasing parity, there is a decrease in the proportion of body fat in the hips and thighs per unit of BMI, while the relative proportion in the waist remains about the same. With age as a covariate, an analysis of

TABLE 1. Beta coefficients for parity in relationship to fat distribution controlled for BMI and age, ages 11–49, NHANES III

Hip circumference (cm)	−0.590*
Thigh circumference (cm)	−0.467*
Arm circumference (cm)	−0.026
Waist circumference (cm)	0.468*
Suprailiac skinfold (mm)	−0.234*
Thigh skinfold (mm)	−1.031*
Triceps skinfold (mm)	−0.252*
Subscapular skinfold (mm)	0.021
Waist/hip ratio	0.007*

*$P < 0.001$.

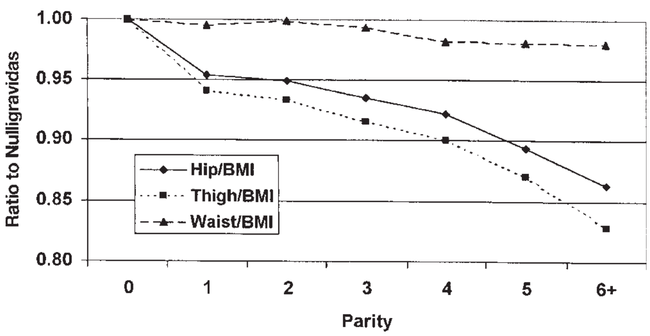

Fig. 2. Ratios of hip, thigh, and waist circumferences to BMI vs. parity for females aged 11–49 years in NHANES III sample (n = 6,753, 0 parity = nulligravida).

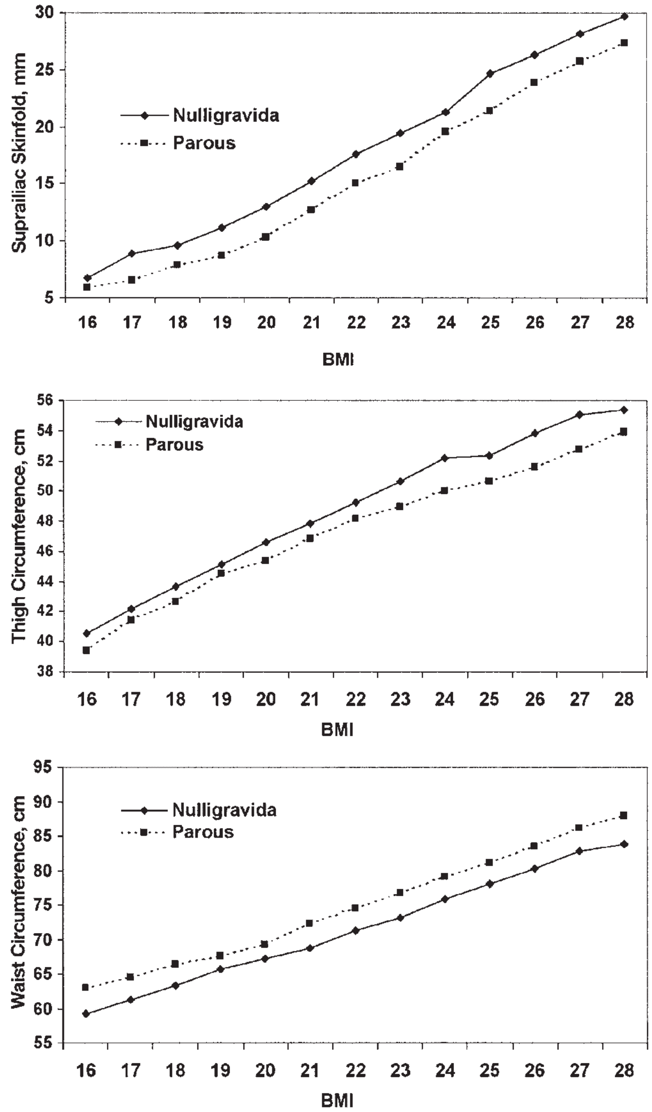

Fig. 3. Selected fat measures for BMIs between 16–28 in nulligravid (n = 1,640) and parous (n = 2,460) women aged 11–49 in NHANES III sample. **a:** Mean suprailiac skinfold thickness (in mm). **b:** Mean thigh circumference (in cm). **c:** Mean waist circumference (in cm).

variance (ANOVA) shows no difference in the ratios for waist/BMI for different parities ($F = 1.530$, $P = 0.164$), but significant differences for hip/BMI ($F = 24.16$, $P < 0.001$) and thigh/BMI ($F = 37.49$, $P < 0.001$).

A third way to explore the relationship of parity to fat distribution is to compare measures of fat storage in parous and nulligravid women with the same BMI. Because the numbers of women with different parities for a given BMI are small, it is most useful to compare all parous women with nulligravidas for ages 11–49. Figure 3 compares the suprailiac skinfold, thigh circumference, and waist circumference in nulligravidas and parous women for different BMI levels. Suprailiac skinfold and thigh circumference are significantly lower for each BMI, while waist circumference is significantly higher in parous women compared with nulligravidas ($P < 0.05$ or less). Using regression to control for BMI, the suprailiac skinfold is 1.61 mm and thigh circumference is 1.41 cm smaller, and waist circumference is 3.26 cm larger, in parous women compared with nulligravidas ($P < 0.001$). Comparing parous women under age 50 with nulligravidas aged 20–24, BMI and waist circumference were 13% higher and estimated fat was 24% higher, but increases in hip (6%) and thigh (3%) circumference were much smaller.

Finally, more direct information on changes in fat distribution in relation to reproduction was provided by those who were pregnant or lactating at the time of the survey. Although sample sizes are small and the data are cross-sectional, they give some insight into how changes in fat distribution related to parity may come about.

Table 2 shows anthropometric data for pregnant and lactating women in the NHANES III sample compared with nulligravidas. The average age of pregnant women was 25.0 ± 6.1 years, and for those lactating, 27.8 ± 5.4 years, and the average parity was 2.2 ± 1.2 (after birth) and 2.2 ± 1.1. (Four women with parities over five were excluded from the lactating group to provide comparability.) For women in months 7 and 8 of pregnancy, daily energy intake was about 2.1 megajoules (MJ) higher than in nulligravidas ($P < 0.01$). Women in month 9 had 5.5 kg more fat than those in the first month, and while fat was higher than in month 8, the hip and thigh circumferences were smaller, suggesting that fat was mobilized from lower-body stores.

Energy intake in lactating women showed a relatively small increase compared with nulligravidas or early pregnancy, and was lower than nulligravidas in later months, although the difference was not significant. Measures of fat storage were lower in women nursing for 7 or more months compared with nulligravidas and pregnant women, with larger differences for the suprail-

TABLE 2. Daily energy intake and measures of fat distribution in pregnant women by month and in lactating females 0–7 and 7–24 months postpartum in NHANES III sample compared with nulligravidas 20–29

	N	MJ/day	Triceps skinfold	Subscapular skinfold	Suprailiac skinfold	Thigh skinfold	Hip circumference	Thigh circumference
Nulligravid	345	8.40	22.0	20.7	23.6	30.3	98.1	51.3
	SD	4.00	9.6	10.9	11.5	12.0	11.8	12.0
Months pregnant								
1	14	9.09	21.8	22.0	21.6	30.2	100.7	51.2
	SD	5.36	10.4	12.1	12.5	14.0	10.1	5.7
2	32	9.00	20.6	19.4	20.5	28.5	98.0	49.8
	SD	3.67	10.3	8.7	10.9	11.8	11.0	7.5
3	39	9.69	21.0	22.3	21.9	31.0	98.9	50.3
	SD	4.36	8.9	10.2	9.9	13.6	10.6	7.5
4	46	8.86	21.8	21.1	23.2	29.2	101.3	50.8
	SD	3.64	10.7	10.1	11.8	12.5	14.6	8.5
5	42	9.10	18.9	20.8	22.6	27.4	98.9	49.7
	SD	3.89	6.7	7.9	9.6	9.4	8.8	5.5
6	28	8.91	24.8	24.7	27.4	32.4	104.5	52.8
	SD	2.73	11.6	12.0	11.3	14.4	13.9	7.9
7	31	10.60	21.0	21.9	26.6	30.2	104.9	52.1
	SD	5.17	8.4	9.2	10.8	12.3	11.9	6.1
8	26	10.45	22.5	23.6	24.5	32.5	108.0	53.1
	SD	4.72	12.1	11.4	11.3	12.1	15.7	8.1
9	19	9.42	23.0	23.7	25.7	32.8	107.8	52.9
	SD	4.16	8.1	11.3	8.8	11.6	9.5	5.7
Lactating								
< 7 months	59	9.30	22.2	22.8	22.9	30.9	100.7	51.0
	SD	3.42	8.9	10.0	9.6	12.1	10.2	6.6
7–24 months	23	8.15	20.4	20.7	19.2	24.2	97.3	49.2
	SD	3.03	7.3	7.9	8.6	8.0	7.5	4.4

iac ($P < 0.05$) and thigh ($P < 0.05$) skinfolds, and hip and thigh circumferences ($P < 0.05$), again indicating more lower-body fat mobilization. They also had 2.1 kg less estimated fat than the nulligravidas ($P < 0.05$).

DISCUSSION

Women in the NHANES III sample stored an average of 16.2 kg of fat by age 17. Like other populations of well-nourished women with relatively long birth intervals, they tended to add additional body fat with each reproductive cycle. Younger parous women weighed 2 kg more than comparably aged nulligravidas, and fat mass was 0.35 kg higher per year ($P < 0.0001$) in parous women from ages 18–34, while there was no significant change in nulligravidas.

Although parous women weighed more than nulligravidas and tended to increase body mass and fat with age, when compared with nulligravidas with the same BMI and age, they had relatively *less* body fat in the hips and thighs, as indicated by smaller suprailiac and thigh skinfolds. Thus, they had a smaller proportion of fat stored in those depots where fat is both stored preferentially during childhood and puberty and protected from mobilization until late pregnancy and lactation. Controlling for age and BMI, there was a small but significant net loss of fat mass with each live birth. We refer to this phenomenon as *covert maternal depletion*. Because the effect is relatively small and because well-nourished women tend to increase body mass with age and parity, the loss of lower-body fat relative to body mass is not readily apparent, and was overlooked in prior research.

Similar evidence for covert maternal depletion in a relatively well-nourished population may be present in a study by Rodrigues and Da Costa (2001) of 203 women in Brasilia, with a mean age of 25–28. They found that while BMI was slightly higher in primiparas compared with nulligravidas (22.1 vs. 21.8), the percent body fat was lower (26.0 vs. 27.2), showing that the effect of pregnancy was to decrease the proportion of body fat in relation to BMI, as in our study.

Looking at changes in fat measures during pregnancy and lactation provides insights into why there is a relative decrease in lower-body fat in women who have given birth. Like other women in well-nourished populations, pregnant women in the NHANES III sample had a larger fat mass than nulligravidas, but there was some indication of a decrease in lower-body fat stores late in pregnancy. Decreases in lower-body fat during the last trimester of pregnancy were also found in Swedish women (Forsum et al., 1989).

In women lactating more than six months, we found that measures of fat storage were lower, but there were greater decreases for lower-body fat measures. Similar decreases in lower-body fat were found in other American samples of lactating women. A Pennsylvania study that compared lactating mothers with those using formula found a greater mobilization of fat in the thighs and hips in lactating women, while there was little difference in upper-body fat (Kramer et al., 1993). A study in Texas found a significant decrease in suprailiac and subscapular skinfolds and a weight loss of 5.3 kg during the first 4 months of lactation, while there was no significant change in biceps or triceps skinfolds (Butte and Garza, 1986). Another Texas study found a decrease in fat of 3.5 kg over 1 year in lactating women, no change in the triceps skinfold, and a 4% increase in the subscapular, a 4% decrease in the suprailiac, and a 10% decrease in the thigh skinfold (Motil et al., 1998).

The decrease in lower-body fat during late pregnancy and lactation is explained by the increased mobilization of fat from these depots due to changes in fat metabolism (Rebuffe-Scrive, 1987). When weight is regained after the postpartum period, relatively more fat is stored in the abdominal and upper body depots, leading to the relative decrease in lower-body fat documented here in the NHANES III population.

Why should fat be stored in such large amounts during childhood and early pregnancy and then be selectively mobilized from the lower body during late pregnancy and lactation, irrespective of current and overall nutritional status and instead of increasing dietary intake?

There are reasons to think that brain development is a limiting life-history variable. Across primates generally, brain growth shows "compensation" between pre- and postnatal phases: species with large-brained neonates show relatively less postnatal brain growth, and species with small-brained neonates show more postnatal brain growth (Harvey et al., 1987). Humans are the only exception, showing extensive pre- and postnatal brain growth. It follows that the demands of building fetal and infant human brains are maximal, and should have shaped supporting metabolic adaptations. During the first year of postnatal life, the brain increases by almost 1 kg (Lauritzen et al., 2001). Mobilized maternal fat may provide critical fatty acids and energy for brain growth.

One kilogram of fat yields approximately 40 MJ of energy, and the additional energy required for lactation for women exclusively breastfeeding was estimated at 2.5–2.8 MJ per day (Dewey, 1997), or an increase of 22–26% over the usual intake (Forsum et al., 1992; Dufour and Sauther, 2002). Why these additional demands could not be met by additional energy consumption, as they are during late pregnancy, is not immediately obvious. Note, for example, that in the NHANES III sample, women in months 7 and 8 of pregnancy had mean daily caloric intakes about 2.1 MJ higher than nulligravidas, but that intake was below that of nulligravidas during lactation. If providing energy to the nursing infant were the main consideration, continuing a high energy intake during lactation would seem to be more adaptive than reducing intake and drawing on lower-body fat stores.

Thus, it seems worthwhile to consider another possible reason for fat storage and mobilization in women: meeting the critical need for certain fatty acids in the rapidly growing fetal and infant brain. A substantial body of evidence suggests that the long-chain polyunsaturated fatty acids (LCPUFA), arachidonic acid (AA) and especially docosahexaenoic acid (DHA), may be limiting resources in neural development. These two LCPUFA each constitute 10% of the dry weight of the human brain. A variety of studies point to better visual, neuro-, and cognitive development in breast-fed infants, in infants fed DHA-enhanced formula, and in singletons as opposed to twins (Broadhurst et al., 2002; Uauy et al., 2001; McFadyen et al., 2001). The concentration of LCPUFA in lower-body fat is higher than in abdominal depots (Phinney et al., 1994).

Although they tend to be overweight, American women are deficient in DHA. The daily adult requirement was estimated to be 220–400 mg (Bjerve et al., 1989; Simopoulos et al., 1999). Based on food brought to market data, the US diet provides only 90 mg of DHA per day (Gerrior et al., 2004). Although DHA can also be synthesized from α-linolenic acid (18:3n-3), linoleic acid (18:2n-6) competes for the enzyme required for this synthesis, and the levels of linoleic acid in the American diet are much higher (32 g/day) than those of α-linolenic (3 g/day). The combination of high linoleic and low DHA in the American diet leads to very low levels of DHA in neonatal cord blood (Minda et al., 2002), milk (Hibbeln, 2002), and stored fat (Nelson et al., 1997; Andersen et al., 1999) compared with most other populations.

The total amount of DHA in the fetus was estimated at 6–10 g, nearly all of which comes from the mother (Clandinin et al., 1981; Haggarty, 2004). An additional 20 g of DHA are excreted in the milk during the first year of nursing (assuming a daily output of 700 g, 4.5% fat, and 0.17% of fat in DHA). Studies using isotope-labeled fatty acids showed that 60–80% of the AA and DHA in breast milk come from maternal fat stores (Hachey et al., 1987; Demmelmair et al., 1998; Del Prado et al., 2000; Fidler et al., 2000).

This means that a total of about 15 g of DHA would be provided by fat stores during the first year, and at 2 g of DHA per kg of fat would require the mobilization of 7.5 kg of fat. This is in fairly close agreement with the estimate of 9.6 kg of fat loss (0.8 kg per month) in affluent populations during the first year of nursing, and is consistent with the decrease in fat seen in lactating women in the NHANES III sample. Both values are well above the 3.5 kg of fat deposited during early pregnancy in well-nourished women (some of which is mobilized in the third trimester), indicating that fat stores from childhood and puberty must also be utilized. This is also shown by lower total fat levels in mothers nursing for more than 6 months than in nulligravidas. Because DHA levels are also lower in stored fat because of dietary factors, there is a need to mobilize even larger amounts of fat to meet the needs of the fetus and infant.

Thus, despite the fact that American women seem quite well-nourished, because they are deficient in DHA, they may require more mobilization of fat to meet the DHA needs of the fetus and infant than mothers in populations with more DHA and less linoleic acid in the diet, and have a greater need to draw on lower-body fat stores laid down in childhood and adolescence.

This perspective suggests a causal link between two distinctive features of our species: the unusually fatty human female body, and the unusually large human brain. If this view is correct, it may be relevant to the evolution of male mate choice, because if women with relatively larger lower-body fat stores have greater reproductive success, then so too will the men who mate with them.

CONCLUSIONS

Controlling for age and BMI, increasing parity in women in the NHANES III sample was associated with a relative decrease in hip and thigh circumferences, in suprailiac and thigh skinfolds, and in body fat estimated from skinfolds, and an increase in waist circumference, resulting in a relative decrease in lower-body fat.

The storing of 10–20 kg of body fat, mainly in the buttocks and thighs, during childhood and puberty, and the mobilization of these stores during late pregnancy and lactation, may help meet the special needs of the developing human brain for essential fatty acids and energy during the time of peak growth, especially in apparently well-nourished women who are relatively deficient in DHA.

ACKNOWLEDGMENTS

We thank David Lawson for assistance with the figures, and Katherine Hanson and three anonymous reviewers for comments on the manuscript.

LITERATURE CITED

Adair LS. 1992. Postpartum nutritional status of Filipino women. Am J Hum Biol 4:635–646.

Adair LS, Bisgrove EZ. 1991. Maternal anthropometry during pregnancy, pregnancy weight gain, and pregnancy outcome. In: Himes J, editor. Anthropometric assessment of nutritional status. New York: John Wiley. p 233–257.

Adair LS, Pollitt E. 1983. Seasonal variation in pre-partum and post-partum maternal body measurements and infants' birth weights. Am J Phys Anthropol 62:325–331.

Adair LS, Pollitt E, Mueller WH. 1984. The Bacon Chow Study: effect of nutritional supplementation on maternal weight and skinfold thickness during pregnancy and lactation. Br J Nutr 51:357–369.

Adams AM. 1995. Seasonal variations in energy balance among agriculturalists in central Mali: compromise or adaptation? Eur J Clin Nutr 49:809–823.

Alam DS, van Raaij JMA, Hautvast JGAJ, Yunus M, Fuchs GJ. 2003. Energy stress during pregnancy and lactation: consequences for maternal nutrition in rural Bangladesh. Eur J Clin Nutr 57:151–156.

Andersen LF, Solvoll K, Johansson LRK, Salminen I, Aro A, Drevon CA. 1999. Evaluation of a food frequency questionnaire with weighted records, fatty acids, and alpha-tocopherol in adipose tissue and serum. Am J Epidemiol 150:75–87.

Barbosa L, Butte NF, Villalpando S, Wong WW, Smith EO. 1997. Maternal energy balance and lactation performance of Mesoamerindians as a function of body mass index. Am J Clin Nutr 66:575–583.

Beazley JM, Swinhoe JR. 1979. Body weight in parous women: is there any alteration between successive pregnancies? Acta Obstet Gynecol Scand 58:45–47.

Belevady B. 1979. Quantity and composition of breast milk in malnourished mothers. In: Hambraeus L, Sjolin S, editors. The mother/child dyad—nutritional aspects. Stockholm: Almqvist and Wiksell. p 62–68.

Bjerve KS, Fischer S, Wammer F, Egeland T. 1989. α-linolenic acid and long-chain ω-3 fatty acid supplementation in three patients with ω-3 fatty acid deficiency. Am J Clin Nutr 49:290–300.

Boot AM, Bouquet J, de Ridder MAJ, Krenning EP, Keizer-Shrama SMPFM. 1997. Determinants of body composition measured by dual-energy x-ray absorptiometry in Dutch children and adolescents. Am J Clin Nutr 66:232–238.

Broadhurst CL, Wang Y, Crawford MA, Cunnane SC, Parkington JE, Schmidt WF. 2002. Brain specific lipids from marine, lacustrine, or terrestrial food resources: potential impact on early African *Homo sapiens*. Comp Biochem Physiol [B] 131: 653–673

Brown JE, Kaye SA, Folsom AR. 1992. Parity-related weight change in women. Int J Obes 16:627–631.

Butte NF, Garza C. 1986. Anthropometry in the appraisal of lactation performance among well-nourished women. In: Hamosh M, Goldman AS, editors. Human lactation 2: maternal and environmental factors. New York: Plenum Publishing Co. p 61–67.

Butte NF, Hopkinson JM. 1998. Body composition changes during lactation are highly variable among women. J Nutr [Suppl] 128:381–385.

Butte NF, Calloway DH, Van Duzen JL. 1981. Nutritional assessment of pregnant and lactating Navajo women. Am J Clin Nutr 34:2216–2228.

Cederlof R, Kaij L. 1970. The effect of childbearing on body weight: a twin control study. Acta Psychiatr Scand [Suppl] 219:47–49.

Chowdhury AKMA. 1987. Changes in maternal nutritional status in a chronically malnourished population in rural Bangladesh. Ecol Food Nutr 19:201–211.

Clandinin MT, Chappell JE, Heim T, Swyer PR, Chance GW. 1981. Fatty acid utilization in perinatal de novo synthesis of tissues. Early Hum Dev 5:355–366.

Del Prado M, Villapando S, Lance A, Alfonso E, Demmelmar H, Koletzko B. 2000. Contribution of dietary and newly formed arachidonic acid to milk secretion in women in low fat diets. Adv Exp Med Biol 478:407–408.

Demmelmair H, Baumheuer M, Koletzko B, Dokoupil K, Kratl G. 1998. Metabolism of U13C-labeled linoleic acid in lactating women. J Lipid Res 39:1389–1396.

Dewey KG. 1997. Energy and protein requirements during lactation. Annu Rev Nutr 17:19–36.

Dufour DL, Sauther ML. 2002. Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. Am J Hum Biol 14:584–602.

Durnin JVGA. 1980. Food consumption and energy balance during pregnancy and lactation in New Guinea. In: Aebi H, Whitehead R, editors. Maternal nutrition during pregnancy and lactation. Bern: Hans Huber. p 86–95.

Durnin JVGA, McKillop FM, Grant S, Fitzgerald G. 1987. Energy requirements of pregnancy in Scotland. Lancet 2:897–900.

Ehrenberg HM, Huston-Presley L, Catalano PM. 2003. The influence of obesity and gestational diabetes mellitus on accretion and distribution of adipose tissue in pregnancy. Am J Obstet Gynecol 189:944–948.

Eveleth PB, Tanner MJ. 1990. Worldwide variation in human growth, 2nd ed. New York: Cambridge University Press.

Fidler N, Sauerwald T, Pohl A, Demmelmair H, Koletzko B. 2000. Docosahexaenoic acid transfer into human milk after dietary supplementation: a randomized clinical trial. J Lipid Res 41:1376–1383.

Fornes NS, Dorea JG. 1995. Subcutaneous fat changes in low-income lactating mothers and growth of breast fed infants. J Am Coll Nutr 14:61–65.

Forsum E, Sadurskis A, Wagner J. 1988. Resting metabolic rate and body composition of healthy Swedish women during pregnancy. Am J Clin Nutr 47:942–947.

Forsum E, Sadurskis A, Wager J. 1989. Estimation of body fat in healthy Swedish women during pregnancy and lactation. Am J Clin Nutr 50:465–473.

Forsum E, Kabir N, Sadurskis A, Westerterp K. 1992. Total energy expenditure of healthy Swedish women during pregnancy and lactation. Am J Clin Nutr 56:334–342.

Friedlaender JS, Rhoads JG. 1982. Patterns of adult weight and fat change in six Solomon Islands societies: a semi-longitudinal study. Soc Sci Med 16:205–215.

Garner P, Smith T, Baea M, Lai D, Heywood DP. 1994. Maternal nutritional depletion in a rural area of Papua New Guinea. Trop Geogr Med 46:169–171.

Gerrior S, Bente L, Hiza H. 2004. Nutrient content of the US food supply, 1909–2000. (Home Economics Research Report No. 56). U.S. Department of Agriculture, Center for Nutrition Policy and Promotion.

Guillermo-Tuazon MA, Barba CVC, van Raaij JMA, Hautvast JGAJ. 1992. Energy intake, energy expenditure, and body composition of poor rural Philippine women throughout the first six months of lactation. Am J Clin Nutr 56:874–880.

Hachey DL, Thomas MR, Emken EA, Garza C, Brown-Booth L. 1987. Human lactation: maternal transfer of dietary triglycerides labeled with stable isotopes. J Lipid Res 28:1185–1192.

Haggarty P. 2004. Effect of placental function on fatty acid requirements during pregnancy. Eur J Clin Nutr 58:1559–1570.

Harris HE, Ellison GTH, Holliday M, Lucassen E. 1997. The impact of pregnancy on the long-term weight gain of primiparous women in England. Int J Obes 21:747–755.

Harvey PH, Martin RD, Clutton-Brock TH. 1987. Life histories in comparative perspective. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T, editors. Primate societies. Chicago: University of Chicago Press. p 181–196.

Hibbeln JR. 2002. Seafood consumption, the DHA content of mother's milk and prevalence rates of postpartum depression: a cross-national, ecological analysis. J Affect Disord 69:15–29.

Huffman SL, Wolff M, Lovell S. 1985. Nutrition and fertility in Bangladesh: nutritional status of nonpregnant women. Am J Clin Nutr 42:725–738.

Hytten FE, Leitch I. 1971. The physiology of human pregnancy, 2nd ed. Oxford: Blackwell.

Jackson AS, Pollock ML, Ward A. 1980. Generalized equations for predicting body density of women. Med Sci Sports Exerc 12:175–182.

Jellife DB, Maddocks I. 1964. Ecologic malnutrition in the New Guinea highlands. Clin Pediatr (Phila) 3:432–438.

Kardjati S, Kunsin JA, de With C. 1990. Energy supplementation in the last trimester of pregnancy in East Java, Indonesia: effect on maternal anthropometry. Am J Clin Nutr 52:987–994.

Keppel KG, Taffel SM. 1993. Pregnancy-related weight gain and retention: implications of the 1990 Institute of Medicine guidelines. Am J Public Health 83:1100–1103.

Kirchengast S, Winkler EM. 1996. Differential fertility and body build in !Kung San and Kavango females from northern Namibia. J Biosoc Sci 28:193–210.

Koop-Hoolihan LE, Van Loan MD, Wong WW, King JC. 1999. Fat mass deposition during pregnancy using a four-component model. J Appl Physiol 87:196–202.

Korn EL, Graubard BI. 1991. Epidemiologic studies utilizing surveys: accounting for the sampling design. Am J Public Health 81:1166–1173.

Kramer FM, Stunkard AJ, Marshall KA, McKinney S, Liebschutz J. 1993. Breast-feeding reduces maternal lower-body fat. JADA 93:429–433.

Kulin HE, Bwibo N, Muttie D, Santer SJ. 1982. The effect of chronic childhood malnutrition on pubertal growth and development. Am J Clin Nutr 36:527–536.

Lauritzen L, Hansen HS, Jorgensen MH, Michaelsen KF. 2001. The essentiality of long chain n-3 fatty acids in relation to development and function of the brain and retina. Prog Lipid Res 40:1–94.

Lawrence M, Lawrence F, Coward WA, Cole TJ, Whitehead RG. 1987. Energy requirements of pregnancy in the Gambia. Lancet 2:1072–1075.

Little MA, Galvin K, Mugambi M. 1983. Cross sectional growth of nomadic Turkana pastoralists. Hum Biol 55:811–830.

Little MA, Leslie PW, Campbell KL. 1992. Energy reserves and parity of nomadic and settled Turkana women. Am J Hum Biol 4:729–738.

Manning-Dalton C, Allen LH. 1983. The effects of lactation on energy and protein consumption, postpartum weight change and body composition of well-nourished North American women. Nutr Res 3:293–308.

McFadyen M, Farquharson J, Cockburn F. 2001. Maternal and umbilical cord erythrocyte omega-3 and omega-6 fatty acids and haemoroheology in singleton and twin pregnancies. Arch Dis Child 88:134–138.

Merchant K, Martorell R, Haas JD. 1990. Consequences for maternal nutrition of reproductive stress. Am J Clin Nutr 52:616–620.

Minda H, Larque E, Koletzko B, Decsi T. 2002. Systematic review of fatty acid composition of plasma phospholipids of venous cord blood in full-term infants. Eur J Nutr 41:125–131.

Motil KJ, Sheng HP, Kertz BL, Montandon CM, Ellis KJ. 1998. Lean body mass of well-nourished women is preserved during lactation. Am J Clin Nutr 67:292–300.

Mueller WH, Reid RM. 1979. Multivariate analysis of fatness and relative fatness. Am J Phys Anthropol 50:199–208.

Nelson GJ, Schmidt OPC, Bartolini GL, Kelley DS, Kyle D. 1997. The effect of dietary docosahexaenoic acid on plasma lipoproteins and tissue fatty acid composition in humans. Lipids 32:1137–1146.

Norgan NG, Ferro-Luzzi A, Durnin JVGA. 1974. The energy and nutritient intake and energy expenditure of 204 New Guinean adults. Philos Trans R Soc Lond [Biol] 268:309–348.

Owa JA, Adejuyigbe O. 1997. Fat mass, fat mass percentage, body mass index, and mid-upper arm circumference in a healthy population of Nigerian children. J Trop Pediatr 43:13–19.

Pagezy H. 1984. Seasonal hunger as experienced by the Oto and Twa women of Ntomba village in the equatorial forest (Lake Tumba, Zaire). Ecol Food Nutr 15:13–27.

Phinney SD, Stern JS, Burke KE, Tang AB, Miller G, Holman RT. 1994. Human subcutaneous adipose tissue shows site-specific differences in fatty acid composition. Am J Clin Nutr 60:725–729.

Piperata BA, Dufour DL, Reina JC, Spurr GB. 2002. Anthropometric characteristics of pregnant women in Cali, Columbia and relationship to birth weight. Am J Hum Biol 14:29–38.

Pond C. 1997. The biological origins of adipose tissue in humans. In: Morbeck ME, Galloway A, Zihlman AL, editors. The evolving female: a life history perspective. Princeton: Princeton University Press. p 147–162.

Prentice AM, Whitehead RG, Roberts SB, Paul AA. 1981. Long term energy balance in child bearing Gambian women. Am J Clin Nutr 34:2790–2799.

Prentice AM, Poppitt SD, Goldberg GG, Murgatroyd PR, Black AE, Coward WA. 1992. Energy balance in pregnancy and lactation. In: Allen L, King J, Lonnerdal B, editors. New York: Plenum Press. p 11–26.

Rebuffe-Scrive M. 1987. Regional adipose tissue metabolism in women during and after reproductive life and in men. Recent Adv Obes Res 5:82–91.

Rebuffe-Scrive M, Enk L, Crona N, Lonnroth P, Abrahamsson L, Smith U, Bjorntorp P. 1985. Fat cell metabolism in different regions in women: effect of menstrual cycle, pregnancy and lactation. J Clin Invest 75:1973–1976.

Rodrigues MLC, Da Costa THM. 2001. Association of the maternal experience and changes in adiposity measured by BMI, waist:hip ratio and percentage of body fat in urban Brazilian women. Br J Nutr 85:107–114.

Rookus MA, Rokebrand P, Burema J, Deurenberg P. 1987. The effect of pregnancy on the body mass index nine months postpartum in 49 women. Int J Obes 11:609–618.

Rossner S. 1992. Pregnancy, weight cycling and weight gain in obesity. Int J Obes 16:145–147.

Schutz Y, Lechtig A, Bradfield RB. 1980. Energy expenditures and food intakes of lactating women in Guatemala. Am J Clin Nutr 33:892–902.

Shell-Duncan B, Yung SA. 2004. The maternal depletion transition in northern Kenya: the effects of settlement, development and disparity. Soc Sci Med 58:2485–2498.

Sidebottom AC, Brown JE, Jacobs DR Jr. 2001. Pregnancy-related changes in body fat. Eur J Obstet Gynecol Reprod Biol 94:216–223.

Simopoulos AP, Leaf L, Salem N Jr. 1999. Workshop on the essentiality of and recommended dietary intakes for omega-6 and omega-3 fatty acids. J Am Coll Nutr 18:487–489.

Singh J, Prentice AM, Diaz E, Coward WA, Ashford J, Sawyer M, Whitehead RG. 1989. Energy expenditure of Gambian women during peak agricultural activity measured by the doubly-labeled water method. Br J Nutr 62:315–329.

Slaughter MH, Lohman TG, Boileu RA, Horswill CA. 1988. Skinfold equations for estimation of body fatness in children and youth. Hum Biol 60:709–723.

Taggart NR, Holliday RM, Billewicz WZ, Hytten FE, Thomson AM. 1967. Changes in skinfolds during pregnancy. Br J Nutr 21:439–451.

Thongprasert K, Tanpaichitre V, Valvyasevi A, Kittigool J, Durnin JVGA. 1987. Energy requirements of pregnancy in rural Thailand. Lancet 2:1010–1012.

Tracer DP. 1991. Fertility-related changes in maternal body composition among the Au of Papua New Guinea. Am J Phys Anthropol 85:393–405.

Tuazon MAG, van Raaij JMA, Hautvast JGAJ, Barra CVC. 1987. Energy requirements of pregnancy in the Philippines. Lancet 2:1129–1133.

Uauy R, Hoffman DR, Peirano P, Birch DG, Birch EE. 2001. Essential fatty acids in visual and brain development. Lipids 36:885–895.
van Raaij JMA, Vermaat-Miedema SH, Schonk CM, Peek MEM, Hautvast JGAJ. 1987. Energy requirements of pregnancy in the Netherlands. Lancet 2:953–955.
Ventkachatalam PS. 1962. A study of the diet, nutrition and health of the people of the Chimbu area (New Guinea Highlands). Port Movesby: Territory of Papua New Guinea Department of Health monograph 4.
Villar J, Cogswell M, Kestler E, Castillo P, Menendez R, Repke RT. 1992. Effect of fat and fat-free mass deposition during pregnancy on birth weight. Am J Obstet Gynecol 167:1344–1352.
Wolfe WS, Sobal J, Olson CM, Frongillo EA, Williamson DF. 1997. Parity-associated weight gain and its modification by sociodemographic and behavioral factors: a prospective analysis in US women. Int J Obes 21:802–810.
Yu DW, Shepard GH. 1998. Is beauty in the eye of the beholder? Nature 396:321–322.