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Carcass and Tissue Fat Content in the Pregnant Rat

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Abstract. The present study in rats was aimed at determining the specific day of pregnancy on which maternal body fat accumulation starts and which tissues are involved. Most of the body weight increase at day 12 of gestation corresponded to conceptus-free maternal weight which progressively increased until the 19th day of gestation after which maternal weight stabilized and the rate of conceptus weight gain became maximal. Maternal carcass fat content progressively increased until day 18 of gestation, increased very markedly on day 19, stabilized between day 19 and 20 and then decreased on day 21. These changes were the opposite of the course of the specific-gravity values. The fresh weight of lumbar fat-pads and mesenteric adipose tissue reflected the changes in carcass fat content throughout gestation. Periuterine adipose-tissue mass declined on day 12 of gestation to be recuperated later, subcutaneous adipose tissue increased on day 12 to decline progressively thereafter and interscapular brown adipose tissue remained stable until day 20 and increased on day 21. With only a few exceptions, the lipid concentration in all these adipose tissues remained stable throughout gestation. Mammary glands and liver weights increased intensely from day 12 and, whereas the lipid concentration in the former was stable, in the latter it decreased on day 12 and increased on days 18 and 19. These results show that in the rat (a) maternal carcass fat accumulation during gestation is not paralleled by the size of the different fat-storing tissues and (b) mammary-gland fat accumulation also contributes to maternal fat storage.

Introduction

Maternal body fat accumulation is one of the most striking features of gestation in both women [1, 2] and experimental animals [3–6]. In pregnant women, body fat accumulation reaches a maximum at mid-gestation and then does not increase any further or declines slightly [1, 2], whereas in the pregnant rat, as we have previously shown, maternal fat accumulation lasts at least as long as day 19 of gestation and declines on day 21 [4, 6]. In the pregnant rat model this biphasic pattern is associated with an early increase in de novo fatty-acid synthesis and heightened glucose incorporation into glyceride glycerol, indicating increased fatty-acid reesterification [7–9] followed by a reduction in these parameters [7, 9] and an increase in adipose-tissue lipolysis [10, 11] resulting in net increase in fat depot breakdown. These changes have an important role in the metabolic adaptations of pregnancy for the mother as well as for the fetus [12], but on what day of gestation they occur and which tissues are involved is not yet well established. Carcass analyses have demonstrated that the 20-hour starved rat has already accumulated fat on day 12 of gestation [3], but this was not the case in fed animals at either day 12 [4] or day 16 of gestation [8]. Although not systematically studied, the contribution of different tissues to maternal fat accumulation substantially differs between tissues and from one author to another. Some authors have shown that one third of the fat accumulated during pregnancy was deposited subcutaneously and the rest in central depots [3] whereas others found no significant increase in the weight of the parametrial pad in pregnant rats even though the subscapular and retroperitoneal pad showed significant increases [14] and there are even others who only found a significant increase in the subscapular fat depot weight [5]. Liver triglyceride concentration was found to be unchanged in 12-day pregnant rats [15] whereas it was lower in pregnant rats from 19 days until parturition [6, 15, 16]. Several of these changes are highly dependent on the feeding condition of the animals since they change in magnitude and even direction under the fasting state, as has been observed in the liver of 19- and 20-day pregnant rats [6, 16, 17].

Since, in the course of gestation, the mother passes through two distinct stages, the first anabolic and the second catabolic [7, 18], it is of interest to know on what specific day of pregnancy maternal body fat accumulation starts and what tissues are involved. The present research investigated this question by systematically measuring the fat content in the total carcass and the lipid concentration in different tissues of the fed pregnant rat on different days of gestation.

Material and Methods

Female Wistar rats from our own colony were fed a Purina chow diet ad libitum (Panlab, Barcelona, Spain) and mated when weighing 160–180 g (the day spermatozoids appeared in vaginal smears was considered day 0 of gestation). Age-matched virgin rats were used as controls. Animals were decapitated by guillotine and their heads discarded.

Carcass specific gravity and fat content were measured as previously described [4]. After killing, body hair was removed with electric clippers and the skin rubbed with a depilatory cream. Lungs, gastrointestinal tract, viscera and conceptus were removed whereas the mesenteric fat remained in each carcass which was suspended from the tail by a silk thread and consecutively weighed both in air and under water (21 °C) until constant weight. Body specific gravity was calculated using the following formula:

$$\text{Specific gravity} = \frac{WA}{(WA - WW)\cdot SG},$$

where WA is carcass weight in air; WW = carcass weight in water, and SG = specific gravity of water at 21 °C (0.9979). After the submerged weight was obtained, each carcass was dried with filter paper and homogenized with a meat mincer. Three 0.5-gram aliquots of these homogenates were used for fat extraction and purification in chloroform-methanol (2:1, by vol) [19]. Lipid extracts from each rat were pooled in

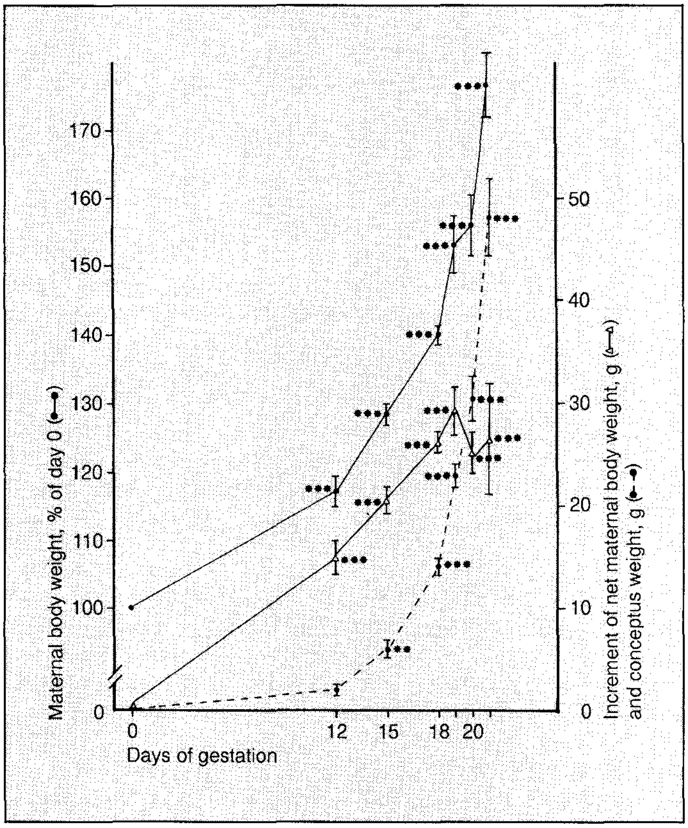

Fig. 1. Maternal body and conceptus weights and increments of net maternal body weight (e.g. conceptus-free weight) in the rat at different times of gestation. Means ± SEM of 5 rats per group. Statistical comparisons versus day 0 are shown by asterisks: ** $p < 0.01$, *** $p < 0.001$.

preweighed vials and allowed to evaporate completely, and the lipid content was measured gravimetrically. When values of the percentage of carcass fat from pregnant rats of 12, 15, 18, 19, 20 and 21 days of pregnancy and virgin rats were plotted against their respective specific gravity, the highly significant linear correlation found (% fat = −274.9 (specific gravity) +304, r = 0.9026, $p < 0.001$) was very similar to that previously reported [4], validating the methodology used and indicating its high sensitivity.

Another series of pregnant and virgin animals were subjected to the same conditions and killed the same way as above, but the liver and white adipose tissue from their lumbar, subcutaneous, periuterus and mesenteric pads, mammary gland and brown interscapular adipose tissue were immediately dissected. Duplicate weighed aliquots were placed into chloroform-methanol for lipid extraction and purification [19], and lipid content was measured gravimetrically.

Results are expressed as mean ± SEM and statistical comparison between groups was done by the Student's t test.

Results

As shown in figure 1, when expressed as percent of values on day 0 of gestation, body weight progressively increased with gestational time and was already significant on day 12 of gestation ($p < 0.001$). Although this change partially corresponds to the increase in conceptus mass, the value of this parameter was practically negligible on day 12, and most of the maternal body weight increase at this gestational time corresponded to conceptus-free maternal weight (fig. 1). As also seen in figure 1, the net maternal body weight increase lasted until the 19th day of pregnancy stabilizing later on. These days of stable net maternal body weight coincide with the maximal rate of conceptus weight accretion (fig. 1).

As shown in figure 2a, when compared to values in virgin controls, maternal carcass fat content slightly although not significantly increased on day 12 of gestation whereas it was already significantly augmented on day 15. This value remained stable between the 15th and 18th days of gestation, increased very markedly on day 19 of gestation, stabilized again between days 19 and 20, and then decreased on day 21, although values were still significantly higher than in virgins (fig. 2a). A similar picture, but oriented in the opposite direction, is seen with specific-gravity values (fig. 2b), which were slightly but not significantly reduced in 12-day pregnant rats, decreased later on with the most striking reduction appearing in 19-day pregnant animals, and then showed a clear tendency to recuperate on days 20 and 21 of gestation.

Table 1 summarizes the weight and lipid concentration of the different adipose tissues determined herein. Lumbar fat-pad weight progressivelly increases until day 20 of gestation and then declines on day 21, although, when compared to values found in virgin controls, the enhancement was only significant on days 15 and 20. Lumbar fat-pad lipid concentration was stable through gestation (table 1). Periuterine adipose-tissue mass declined significantly on day 12 of gestation whereas later on the values recuperated and did not differ from those in virgins (table 1). The lipid concentration in these tissues was very stable throughout gestation and values did not differ between the groups (table 1). The mesenteric adipose-tissue mass remained stable until the 15th day of

Table 1. Effect of gestational time on different adipose tissue depots in the rat

		Lumbar fat-pads		Periuterine adipose tissue	
		weight[a]	lipids[a]	weight	lipids
Virgins		1.69±0.05	0.586±0.046	4.58±0.25	0.579±0.073
Pregnants	Day 12	1.52±0.27	0.582±0.018	2.77±0.29**	0.640±0.020
	Day 15	2.11±0.16*	0.569±0.043	4.36±0.24	0.547±0.020
	Day 18	1.82±0.07	0.608±0.033	3.90±0.25	0.569±0.048
	Day 19	2.11±0.24	0.623±0.022	5.00±1.31	0.540±0.019
	Day 20	3.00±0.19***	0.540±0.076	3.41±0.52	0.419±0.079
	Day 21	2.00±0.18	0.588±0.021	5.48±0.83	0.574±0.052

Means ± SEM of 5 rats per group. Statistical significance of the difference versus virgins is shown by asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; no asterisk = not significant.

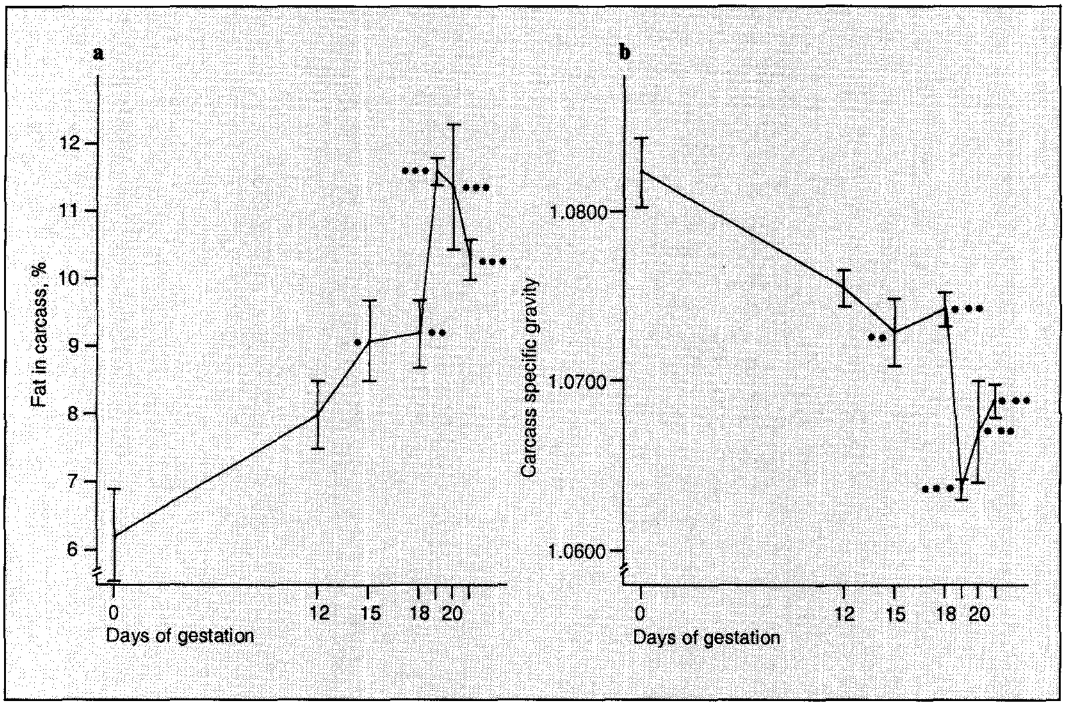

Fig. 2. Maternal carcass fat content (**a**) and specific gravity (**b**) in the rat at different times of gestation. Means ± SEM of 5 rats per group. Statistical comparisons versus day 0 are shown by asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Mesenteric adipose tissue		Subcutaneous adipose tissue		Interscapular brown adipose tissue	
weight	lipids	weight	lipids	weight	lipids
2.33±0.20	0.489±0.045	3.40±0.12	0.377±0.075	0.41±0.04	0.161±0.030
2.79±0.48	0.450±0.034	4.49±0.48*	0.129±0.010*	0.30±0.02	0.145±0.009
2.66±0.29	0.600±0.031	3.63±0.28	0.212±0.039	0.40±0.02	0.185±0.019
3.89±0.38**	0.513±0.010	3.12±0.21	0.357±0.041	0.44±0.01	0.137±0.017
3.53±0.22**	0.506±0.058	2.89±0.31	0.271±0.052	0.49±0.04	0.159±0.026
3.28±0.26*	0.532±0.026	2.54±0.21**	0.703±0.017**	0.47±0.05	0.265±0.025*
3.14±0.38	0.479±0.037	2.90±0.29	0.180±0.034*	0.53±0.05*	0.115±0.025

[a] Weight in grams and lipids in grams per gram of tissue.

Table 2. Effect of gestational time on mammary gland and liver mass and lipid concentration in the rat

		Mammary glands		Liver	
		weight, g	lipids, g/g tissue	weight, g	lipids, g/g tissue
Virgins		1.21±0.04	0.370±0.101	7.05±0.63	0.027±0.003
Pregnants	Day 12	3.64±0.25***	0.199±0.034	10.58±0.76*	0.018±0.002*
	Day 15	7.64±0.27***	0.202±0.024	11.52±0,41***	0.023±0.002
	Day 18	9.86±0.19***	0.150±0.036	12.58±0.61***	0.037±0.003*
	Day 19	8.81±0.68***	0.233±0.038	12.28±0.88***	0.039±0.003*
	Day 20	11.25±0.84***	0.231±0.017	12.58±1.09***	0.034±0.005
	Day 21	10.56±0.98***	0.167±0.028	13.04±0.58***	0.026±0.003

Means ± SEM of 5 rats per group. Statistical significance versus virgins is shown by asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; no asterisk = not significant.

gestation, increased significantly on day 18, remained elevated until day 20, and slightly decreased on day 21 when the value no longer differed statistically from that of the virgins (table 1). The lipid concentration in the mesenteric adipose tissue did not change in pregnant rats when compared to virgin controls (table 1). Subcutaneous adipose tissue significantly increased in pregnant rats on day 12 of gestation, progressively declining thereafter until values on day 20 were significantly lower than those of virgin rats (table 1). Whereas the lipid concentration in subcutaneous adipose tissue was significantly reduced on day 12 of gestation, values were very similar in virgin animals and pregnant ones at 15, 18 and 19 days of gestation, and there is a sharp increase on day 20 followed by a decrease on day 21 (table 1), indicating a body redistribution of these fat depots. Interscapular brown adipose tissue remains stable until the 20th day of gestation and then significantly increases on day 21 (table 1). Like in subcutaneous adipose tissue, the lipid concentration in interscapular brown adipose tissue increased on day 20 as compared to the value on the previous gestational day, and decreased on day 21 (table 1).

Tissue weight and lipid concentration in the mammary gland and liver are shown in table 2. At 12 days of gestation there was an intense and significant increase in mammary-gland mass already. This parameter increased progressively until day 20 of gestation at which time it stabilized (table 2). Mammary-gland lipid concentration decreased on day 12 of gestation and remained lower than in virgin animals throughout gestation, although the differences were not statistically significant due to the high variation of the values in virgin animals (table 2). Liver weight also increased significantly on day 12 of gestation and continued to increase progressively with gestational time (table 2). Liver lipid concentration decreased on day 12 of gestation and increased on days 18 and 19, whereas values on days 20 and 21 no longer differed from those of virgins (table 2).

Discussion

Present findings extend previous reports showing an increase in fat depots during pregnancy in the rat [3–6] by specifically determining the precise gestational day on which these changes occur. By studying both specific gravity and lipid content in carcasses, our results show that maternal fat stores in the fed pregnant rat accumulate slowly and progressively up to the 18th day of gestation and then increase quite sharply on days 18 and 19. Maternal body fat content stays at the maximum level through day 20 and then begins declining on day 21. This condition is responsible for the cessation of maternal body weight increase occurring during the last days of pregnancy. Independently of their physiological significance, these changes must be the result of the juxtaposing effects of several factors. Since maternal food intake, the level of circulating lipids [15] and the rate of lipogenesis [8] are still unmodified on day 12 of gestation, initiation of body fat accumulation at this time may be caused by the increase in extrahepatic tissue lipoprotein lipase activity [20]. This change disappears on day 15 of gestation [20] but the circulating triglycerides are already high [21] and since the K_m of adipose-tissue lipoprotein lipase is higher than the plasma triglyceride concentration [22], the change may facilitate its catalytic action and therefore enhance lipid uptake by maternal adipose tissue. Besides this, at this stage of gestation both maternal food intake [20] and adipose-tissue lipogenesis are enhanced [8], and these factors may also contribute to the progressive accumulation of maternal fat depots. There are no substantial changes in these parameters in the mother on days 18 and 19 that would justify the sharp increase in fat deposition found at this time. At this stage of gestation there is even a decrease in adipose-tissue lipoprotein lipase [20, 23–25] which could indicate a decreased tissue uptake of circulating triglycerides. However, the overproduction of endogenous triglycerides [21] as well as the enhanced arrival to circulation of dietary lipids [26] cause intense maternal hypertriglyceridemia which could compensate for the reduced lipoprotein lipase activity and allow even an enhanced uptake of circulating triglycerides by adipose tissue [26]. Nevertheless, another change in the maternal adipose-tissue metabolism could contribute to such exaggerated fat deposition occurring between days 18 and 19. At this stage of gestation, metabolism of white adipose tissue is greatly accelerated, as shown by an increase not only in lipogenesis but also in the esterification of free fatty acids, and these changes may exceed the augmented lipolytic activity [9] allowing a rapid net deposition in the fat depot. This interpretation fits well with our finding of a decline in fat accumulation on 21 days of gestation, since it has previously been found that there is a sharp reduction in both white adipose-tissue fatty-acid esterification and synthesis [9] coincident with a lack of lipoprotein lipase activity [24] at this stage, while lipolytic activity is still very active and would cause depletion of maternal fat depots.

The present study also shows that although total lipid concentration in most maternal adipose tissues are kept relatively stable throughout pregnancy, those changes in maternal carcass fat content are not reflected in a similar manner in the size of the different fat-storing tissues. Thus, whereas on day 12 of gestation there is a decline in periuterine adipose-tissue mass, this is compensated for by an increase in subcutaneous adipose tissue, and later, the mass of mesenteric adipose tissue and mammary glands are the ones that most similarly parallel the changes found in the amount of fat present in the carcass. At the 20th day of gestation there is a sharp increase in lumbar fat adipose-tissue mass with a reduction at day 21, and this could also contribute to the changes found in the fat content of the carcass. Interscapular brown adipose-tissue mass remained stable just until 20, enhancing on day 21 which would indicate some relationship with the parturition process, since it is known that the mass of this tissue in the rat declines after this stage [27]. This different distribution of fat depots throughout pregnancy agrees with the known independent metabolic response to the same stimulus by the different adipose tissues in the body [28], although we do not know the nature of the factors behind the specific changes in the different maternal adipose tissues.

Decreased liver lipid concentration on the 12th day of gestation found here is compensated by the greater size of this organ which means that the total lipid content is unchanged [data not shown] whereas later on the amount of lipids present in the liver is clearly higher. The liver is the main receptor organ for adipose-tissue-derived free fatty acids [29] and adipose-tissue lipolysis is greatly enhanced during late gestation [10, 11] causing an enhanced arrival of circulating fatty acids to the liver for triglyceride synthesis. An increased synthesis of triglycerides has been shown in the perfused pregnant rat liver [21], and triglyceride accumulation in the liver does not become more manifest because this effect is compensated by an enhanced triglyceride output [21].

Present findings also show that mammary-gland fat accumulation also contributes to maternal fat storage. This change is specially striking during late gestation and may be related to the enhanced uptake of circulating triglycerides by mammary glands [26] for incorporation into milk lipids which is facilitated by the increase in lipoprotein lipase activity that occurs in these glands of pregnant animals 2–3 days before parturition [24, 30, 31].

The physiological role of most of the observed changes in specific fat storage sides occurring at certain phases of gestation remains to be established. We have previously found that maternal hypothyroidism during the first half of gestation in the rat compromises both maternal liver and conceptus-free body weight increases and fetal growth, and this effect is not compensated for, even when animals received substitution doses of exogenous thyroxine during the second half of gestation [18]. Since we have seen here that a great proportion of the conceptus-free maternal body weight increase corresponds to fat, and since hypothyroidism impairs adipose-tissue development in the nonpregnant rat [32, 33], we propose that body fat accumulation occurring during the second half of gestation is, at least in part, a consequence of metabolic changes occurring during the earlier phase, and that, although it is known that lipids can only cross the placental barrier with difficulty [12], the maternal accumulation of fat stores are of essential importance not only to maternal metabolism but to fetal development.

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