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Maternal Tissue Repartitioning in Pregnant Primiparous Swine in Response to Restriction of Calories or Feed (42717)

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Abstract. Crossbred (Chester White × Landrace × Large White × Yorkshire) primiparous gilts were fed daily a corn–soybean meal-based gestation diet at 1.8 kg (C) or 0.6 kg (R) (6000 or 2000 kcal calculated digestible energy, DE) or a high-protein diet (RCal) at 0.6 kg (2000 kcal calculated DE) from day of mating to slaughter at 100 to 106 days of gestation. The RCal diet contained three times the concentrations of protein and of mineral and vitamin supplement present in the C diet. Body weight and ultrasonically estimated backfat depth were recorded at 0, 4, 8, and 12 weeks postcoitum. The results showed differential effects of form of diet restriction (R vs RCal) on body weight, backfat depth, relative and absolute uterine weight, and on relative kidney, stomach, and trimmed wholesale cut weights of the dam. Maternal and fetal plasma glucose and urea-N concentrations were higher in RCal than in R groups. Total uterus plus gastrointestinal tract relative weight, with or without fetuses, was lower in RCal than in R and C gilts. The ratio of uterus (with or without fetuses) weight to gastrointestinal tract weight was greater in R than in C or RCal gilts. The data are interpreted to indicate that restriction of carbohydrate-fat calories only compared with restriction of a standard diet throughout gestation in swine had a negative effect on uterine growth associated with repartitioning of nutrients to visceral organ and lean tissue growth at the expense of maternal uterine tissue and body fat conservation. © 1988 Society for Experimental Biology and Medicine.

Growth responses of the gastrointestinal tract, reproductive tract, and developing fetus to maternal dietary restriction postcoitum in mammals are not well known. Severe feed restriction (2000 kcal DE daily) throughout pregnancy is compatible with fetal survival in primiparous gilts (1). Litter size appears to be relatively refractory to maternal feed intake (2–5) but fetal growth is decreased by severe feed restriction during pregnancy (3, 6–9). Fetal weight is closely associated with uterine weight at the site of placental attachment and with allantoic and amniotic fluid volumes and fetal membrane weight (10). Positive correlations exist between placental blood flow and placental weight, placental blood flow and fetal weight, and placental weight and fetal weight (11); low birth weight is associated with a small placenta and low placental blood flow (12).

Koong *et al.* (13, 14) provided evidence that feed restriction reduces visceral weight in swine and that the metabolically active visceral organs contribute disproportionately to energy expenditure (15–19). Calorie restriction of carbohydrate and fat (nonprotein) compared with restriction of intake of a balanced diet in young adult rats is associated with a smaller reduction in total gastrointestinal weight and consequently a greater increase in relative weight (percentage of body weight) of total gastrointestinal tract (1). The reduced absolute weight of the maternal gastrointestinal tract during severe feed restriction observed in the rat experiments reported by Pond *et al.* (20) agrees with the work of Koong *et al.* (13, 14) in pigs.

We are unaware of published reports of the relative responses of the gastrointestinal tract of pregnant animals to restricted feed versus restricted carbohydrate and fat calorie intake. Pond *et al.* (1) observed a reduction in absolute weight, but no change in relative weight of visceral organs of pregnant gilts severely restricted in feed intake during the entire gestational period; reproductive tract absolute weight tended to be reduced and relative weight tended to be increased.

The purpose of the present experiment was to test the hypothesis that restriction of carbohydrate and fat calories only versus comparable restriction of a balanced diet throughout gestation produces differential effects on the gastrointestinal tract, repro-

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ductive tract, and body fat and lean tissue of the pregnant primiparous gilt and on growth of the fetuses.

Experimental Procedure. Primiparous crossbred (Chester White × Landrace × Large White × Yorkshire) gilts 7 to 8 months of age, weighing 112.6 kg (range 95.7–132.0 kg) were fed a standard finishing diet *ad libitum* until breeding. On the day of mating they were assigned in sequence to one of three dietary treatments: (1) adequate diet, C, containing 83.9% corn, 11.2% soybean meal, and 4.9% mineral and vitamin supplements (6000 kcal DE, 1.8 kg daily); (2) severe diet restriction, R (2000 kcal DE, 0.6 kg daily); (3) restriction of carbohydrate–fat calories only, RCal (2000 kcal DE, 0.6 kg daily), by feeding a high-protein diet (0 corn, 84.3% soybean meal, and 3% soybean oil) containing three times the concentration of protein and of mineral element and vitamin supplement present in the adequate (C) diet. All gilts were kept in individual stalls (0.3 × 2.3 m) with concrete slotted floors in a light- and temperature-controlled (12 hr light, 12 hr dark; 22 ± 5°C) well-ventilated building and fed their respective diets in meal form once daily to slaughter at 100 to 106 day of pregnancy. Daily intake of gilts fed R and RCal diets was increased on Day 94 of pregnancy to 0.9 kg and continued at that level to the end of the experiment to minimize the rapid weight loss in RCal gilts observed beginning on day 84.

Body weight and ultrasonically determined[1] backfat depth 5 cm off the dorsal midline approximately at the first rib, last rib, and last lumbar vertebra locations were recorded at 4-week intervals throughout the experiment (to Week 12 for backfat and Week 14 for body weight). At approximately Week 15 (Days 100 to 105 for C, Days 101 to 106 for R, and Days 101 to 106 for RCal) all gilts were euthanized by electrical stunning and exsanguination. Blood from severed neck vessels was collected into heparinized, Na-fluoride-containing tubes and placed on ice, hematocrit was measured, and plasma was removed by centrifugation and frozen at −40°C until analyzed for glucose, urea-N, protein, albumin, Ca, inorganic P and Mg[2]. Reproductive and gastrointestinal tracts were removed within 20 min after death. Weights of empty stomach, small intestine, cecum-colon, and of heart, liver and kidneys were recorded. Reproductive tract of each gilt, including ovaries, was weighed unopened. After weighing, blood was collected from the severed umbilical cord of two fetuses (anterior positions 2 and 3 in left uterine horn) into heparinized Na-fluoride-containing tubes and placed on ice, and hematocrit and plasma metabolites[2] were measured as for dams. Fetuses and mummified fetuses in each litter were counted and weighed. Empty uterine weight plus ovaries, placental membranes, cervix and vagina minus fetuses and uterine, allantoic, and amniotic fluids was recorded for each dam. The difference between the weight of the unopened reproductive tract and that of the empty ovaries–uterus–cervix–vagina plus placenta (hereafter referred to as uterus) of each dam was assumed to be the allantoic, amniotic, and uterine fluids. Ratios of uterus to gastrointestinal tract were calculated based on full and empty uterus with or without fluids.

Chilled carcass weight, carcass length (anterior edge of first rib to pubic bone), and weights of trimmed lean tissues (Boston butt, picnic, loin, and ham) were recorded. Cross-sectional areas of the longissimus muscle and of the subcutaneous fat at the 10th–11th rib interface were traced on acetate paper and measured planimetrically.

All data were subjected to least-squares mean analysis of variance (21). For gilt blood, backfat, carcass traits, and body weight, individual animal was the experimental unit; for reproductive and fetus traits, litter was the experimental unit. For gilt body weight and backfat data, gestational stage (time) was included in the model in a split plot analysis of variance.

Results. As expected, body weight of C gilts was greater than that of other gilts (C > R = RCAl); C gilts gained weight steadily during gestation, while R and RCal gilts

[1] Scanoprobe Model 731A, Ithaco, Inc., Ithaca, New York 14850.

[2] Gilford Diagnostics, 16035 Industrial Parkway S.W., Cleveland, Ohio 44135.

gradually lost weight, resulting in a time × diet interaction (Fig. 1). Backfat followed similar trends such that C gilts increased while R and RCAl gilts decreased, resulting in significant effects of diet, time, and diet × time. RCal gilts had less backfat depth ($P < 0.01$) than R and R less ($P < 0.01$) than C gilts (Fig. 1). Backfat and body weight at slaughter were less in RCAl than in R gilts and less in R than in C gilts ($P < 0.01$). Carcass length and absolute weights of trimmed lean tissue, and longissimus muscle and fat area were less ($P < 0.01$) in R and RCal than in C gilts. Mean carcass length, weight of trimmed lean tissues, longissimus muscle cross-sectional area at the 10th–11th rib interface, and fat cross-sectional area at the 10th–11th rib interface for C, R, and RCal gilts were, respectively, 88.4, 83.9, 81.8 cm (C > R = RCal, $P < 0.01$); 27.9, 20.9, 20.6 kg (C > R = RCal, $P < 0.01$); 37.0, 30.3, 32. 7 cm^2 (C > R = RCal, $P < 0.01$) ; 52.1, 25.8, 20.7 cm^2 (C > R > RCal, $P < 0.01$). Relative weights (percentage of body weight) of the sum of the four trimmed lean tissues were similar in C and R gilts but values for RCal gilts were higher ($P < 0.01$) than those in other gilts (18.6, 18.7, and 19.9%, respectively, C = R < RCal).

Control gilts had larger absolute weights of heart, liver, kidneys, stomach, small intestine, cecum-colon, and total gastrointestinal tract than did R and RCal gilts (C > R = RCal), but when expressed as relative weights (percentage of body weight) RCal gilts had heavier kidneys ($P < 0.01$) and stomach ($P < 0.02$) than other gilts and, while not significant, weights of all other organs showed the same trend (Table I).

The effect of gestational diet treatment on reproductive performance and organ weights is summarized in Tables II, III, and IV. Severe restriction of feed or of only carbohydrate and fat calories had no adverse effects on litter size and the number of mummified fetuses. Number of live fetuses and total number of fetuses per litter were similar in C and RCAl gilts and were statistically greater ($P < 0.03$ and 0.02, respectively) in R gilts although, in the context of current knowledge, the result has little biological meaning except to support the concept that reproductive performance is relatively refractory to severe feed restriction in pregnant swine. For

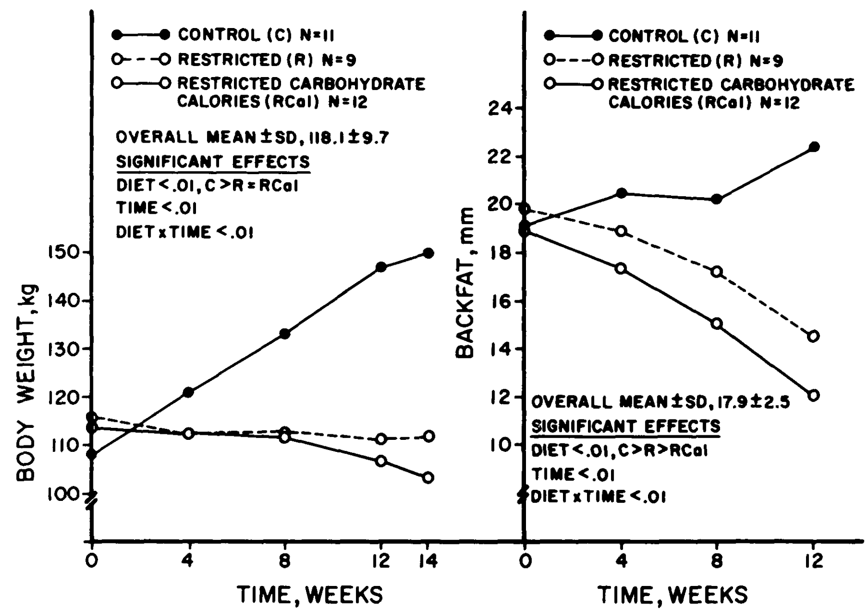

FIG. 1. Effect of swine gestation diet on body weight (left panel) and backfat depth (right panel). Diet regimen labeled restricted carbohydrate calories (RCal) is referred to in the text as restricted carbohydrate and fat calories.

TABLE I. EFFECT OF SWINE GESTATION DIET ON VISCERAL ORGAN WEIGHTS

Organ	Diet C	Diet R	Diet RCal	Overall mean ± SD	Probability
No. of animals	11	9	12		
Slaughter wt (kg)	149.9[a]	112.1[b]	103.4[c]	121.0 ± 8.6	<0.01
Heart (g)	377[a]	329[b]	315[b]	340 ± 5.1	<0.02
Heart (% body wt)	0.241[a]	0.292[b]	0.304[b]	0.283 ± 0.032	<0.01
Liver (g)	1531[a]	1026[b]	1089[b]	1223 ± 208	<0.01
Liver (% body wt)	1.023	0.914	1.049	1.002 ± 0.147	NS
Kidney (g)	253[a]	188[b]	255[a]	224 ± 35	<0.01
Kidney (% body wt)	0.169[a]	0.168[a]	0.216[b]	0.186 ± 0.023	<0.01
Stomach (g)	605[a]	453[b]	492[b]	520 ± 80	<0.01
Stomach (% body wt)	0.404[a]	0.406[a]	0.476[b]	0.432 ± 0.062	<0.02
Small intestine (g)	756[a]	596[b]	582[b]	648 ± 171	<0.05
Small intestine (% body wt)	0.504	0.532	0.570	0.536 ± 0.127	NS
Cecum-colon (g)	1360[a]	944[b]	989[b]	1104 ± 246	<0.01
Cecum-colon (% body wt)	0.907	0.843	0.955	0.907 ± 0.181	NS
Total GI tract (g)	2721[a]	1993[b]	2027[b]	2263 ± 414	<0.01
Total GI tract (% body wt)	1.815	1.781	1.975	1.862 ± 0.310	NS

[a,b,c] Means in the same row without a common superscript differ significantly.

reproductive and organ weight traits, litter size was inserted into the model as a covariate. The only traits found to be affected differently by inclusion of litter size as a covariate were total litter and individual live fetus weight (Table II), empty uterus plus fetuses as a percentage of body weight (Table III), and ratio of uterus plus fetuses to gastrointestinal tract and uterus to gastrointestinal tract weight (Table IV). Other traits listed in Tables II through IV were unaffected by including litter size as a covariate in the analysis. Individual live fetus weight and total litter weight were higher ($P < 0.01$) in C and R than in RCAl groups (C = R > RCal).

Weights of empty uterus plus fetuses and empty uterus minus fetuses, as affected by maternal gestation diet, are shown in Table III. Empty uterus weight plus fetuses and empty uterus weight minus fetuses were less ($P < 0.01$) in RCal than in C and R gilts (RCal < C = R). When expressed as relative weight (percentage of body weight), empty uterus weight plus fetuses was greater ($P < 0.01$) in R than in C and RCal gilts (R > C = RCAl) due to the presence of more fetuses,

TABLE II. EFFECT OF GESTATION DIET TREATMENT ON REPRODUCTION

Organ	Diet C	Diet R	Diet RCal	Oveall mean ± SD	Probability
No. of litters	11	9	12		
Litter size (No.)[a]	8.82[b]	11.67[c]	8.33[b]	9.22 ± 2.59	<0.02
Live fetuses (No.)	8.73[b]	11.33[c]	8.08[b]	9.44 ± 2.77	<0.03
Mummified fetuses (No.)	0.09	0.33	0.25	0.22 ± 0.56	NS
Total live fetus wt (kg)	7.302[b]	8.090[b]	5.395[c]	6.808 ± 1.662	<0.01
Individual live fetus wt (kg)	0.871[b]	0.727[c]	0.665[c]	0.753 ± 0.120	<0.01

[a] Anaysis of the data using number of pigs per litter (litter size) as a covariate in the statistical model to standardize litter size resulted in the following values for C, R, and RCal groups, respectively: litter size, 9.33, 9.45, 9.52; overall mean 9.44 ± 0.56; no significant differences among means (NS). Total live fetus weight, 7.569, 6.941, 6.012, overall mean 6.808 ± 0.896, C = R > RCal ($P < 0.01$); individual live fetus weight, 0.862, 0.775, 0.640, overall mean 0.753 ± 0.107, C = R > RCal ($P < 0.01$). Treatment differences for other traits were unchanged by covariance.
[b,c] Means in the same row without a common superscript differ significantly.

TABLE III. EFFECT OF SWINE GESTATION DIET ON WEIGHT OF GRAVID AND EMPTY UTERUS (OVARIES, UTERUS, CERVIX, AND VAGINA)

Organ	Diet			Overall mean ± SD	Probability
	C	R	RCal		
No. of animals	11	9	12		
Empty uterus + fetus wt (kg)[a]	14.505[b]	15.926[b]	10.998[c]	13.515 ± 3.44	<0.01
Empty uterus + fetus wt (% body wt)[a]	9.667[b]	14.182[c]	10.603[b]	11.194 ± 2.839	<0.01
Empty uterus wt (kg)[a]	5.386[b]	5.784[c]	4.109[c]	5.019 ± 1.052	<0.01

[a] Analysis of the data using number of pigs per litter as a covariate in the statistical model to standard litter size resulted in the following values for C, R, and RCal groups, respectively: empty uterus plus fetuses weight, 15.008, 13.568, 12.110, overall mean 13.515 ± 2.49, C = R > RCal ($P < 0.04$); empty uterus plus fetuses weight (% body wt), 10.059, 12.339, 11.472, overall mean 11.194 ± 2.15; no significant differences among means ($P < 0.01$); empty uterus weight, 5.525, 5.188, 4.429, overal mean 5.019 ± 0.769, C = R > RCal ($P < 0.01$).

[b,c] Means in the same row without a common superscript differ significantly (<0.01).

but when litter size was included in the statistical model as a covariate, maternal diet effects were not significant ($P > 0.10$).

Effects of gestation diet on combined reproductive and gastrointestinal tract weights and the ratio of uterus weight, with and without fetuses, to gastrointestinal tract weight are summarized in Table IV. Combined absolute weights of gastrointestinal tract and uterus, excluding fluids or fluids plus fetuses or including both fluids and fetuses, were less ($P < 0.01$) in RCal than in C or R gilts (RCal < C = R). However, relative weights were greater ($P < 0.01$) in R than in

TABLE IV. EFFECT OF SWINE GESTATION DIET ON WEIGHT DISTRIBUTION AMONG FETUSES, UTERUS (OVARIES, UTERUS, CERVIX, AND VAGINA) AND GASTROINTESTINAL TRACT

Organ	Diet			Overal mean ± SD	Probability
	C	R	RCal		
No. of litters	11	9	12		
Total uterus (fetuses, fluids, uterus) + GI tract (kg)	17.227[b]	17.928[b]	13.532[c]	16.059 ± 3.242	<0.01
Total uterus + GI tract (% body wt)	11.482[b]	15.964[c]	13.091[b]	13.267 ± 2.537	<0.01
Uterus + fetuses + GI tract (excluding fluids) (kg)	15.410[b]	15.867[b]	11.957[c]	14.317 ± 2.404	<0.01
Uterus + fetuses + GI tract (excluding fluids) (% body wt)	10.274[b]	14.186[c]	11.577[b]	11.872 ± 1.811	<0.01
Uterus + GI tract (excluding fluids and fetuses) (kg)	8.108[b]	7.777[b]	6.266[c]	7.358 ± 1.020	<0.01
Uterus + GI tract (excluding fluids and fetuses) (% body wt)	5.411[b]	6.958[c]	6.075[d]	6.096 ± 0.795	<0.01
Uterus + fetuses/GI tract[a]	4.861[b]	6.989[c]	5.147[b]	5.580 ± 1.517	<0.01
Uterus/GI tract[a]	2.069[b]	2.915[c]	2.190[b]	2.358 ± 0.670	<0.02

[a] Analysis of the data using number of pigs per litter as a covariate in the statistical model to standardize litter size resulted in the following values for C, R, and RCal groups, respectively: uterus + fetuses/GI tract, 5.143, 6.100, 5.592, overall mean 5.580 ± 1.004 (no significant treatment effects, $P < 0.16$) and uterus/GI tract, 2.175, 2.581, 2.357, overall mean 2.358 ± 0.520 (no significant treatment effects, $P < 0.29$). Treatment differences for other traits were unchanged by covariance.

[b,c,d] Means in the same row without a common superscript differ significantly.

C and RCal gilts (R > C = RCal, except in the case of the gastrointestinal tract plus uterus, excluding fluids and fetuses, in which R > RCal > C). The ratio of uterus weight, with or without fetuses, to gastrointestinal weight was greater ($P < 0.02$) in R than in C and RCAl gilts (R > C = RCal), but the maternal diet effects were not significant ($P > 0.10$) when litter size was adjusted by covariance.

Maternal hematocrit and plasma concentrations of Ca and inorganic P were not affected by diet; plasma glucose ($P < 0.06$) and urea-N ($P < 0.01$) were higher in RCal than in C and R gilts (133.6, 114.0, and 110.0 mg/dl for glucose and 24.6, 10.1, and 7.6 mg/dl for urea-N, respectively). Plasma protein ($P < 0.07$) and plasma albumin ($P < 0.03$) were less in R than in C and RCal dams (7.24, 7.65, and 7.84 mg/dl and 3.29, 2.97, and 3.2 mg/dl, respectively). Plasma Mg was higher in RCal than in C and R dams (2.4, 2.2, and 2.1 mg/dl, respectively). Fetal plasma glucose tended to be higher in RCal than in C and R progeny (184.1, 139.9, and 128.0 mg/dl, respectively, $P < 0.09$) and plasma urea-N was significantly higher (28.6, 16.2, and 11.6 mg/dl for RCal, C, and R progeny, respectively, $P < 0.01$). Plasma Mg, albumin, and blood hematocrit were unaffected by maternal diet, while plasma protein was higher in fetuses from C than from R or RCal dams (2.07, 1.94, and 1.83 mg/dl, respectively, C > R = RCal, $P < 0.01$). Fetuses from C dams had higher plasma inorganic P than those from R dams (10.2, 9.0, and 9.7 mg/dl for C, R, and RCal dams, respectively, R < C = RCal, P < 0.03).

Discussion. The results show that composition of the diet of pregnant swine restricted in feed intake throughout gestation affects organ weights and indices of body composition of the dam. Increases in relative weights of trimmed lean tissues, kidney, and stomach and a trend toward increases in heart, liver, small intestine, and cecum-colon were observed in primiparous gilts fed restricted carbohydrate and fat calories (RCal) compared with those of gilts fed a restricted amount of a balanced control diet (R) or the NRC (22) recommended level of the control diet (C). The increased visceral organ weight observed here supports the previous observation (20) made in young adult rats fed restricted nonprotein calories. The reduction in absolute weights of visceral organs in animals fed restricted amounts of feed (both R and RCal gilts) was expected (13, 14). These data demonstrate that diet composition affects the response independent of total weight or volume of feed ingested. The physiological basis for this differential response in the relative size of visceral organs in animals fed restricted amounts of feed versus restricted amounts of a diet supplying restricted calories from carbohydrate and fat but quantities of protein, vitamin, and mineral elements equal to those supplied daily to control animals fed C diet is unclear. Lipkin (23) and Johnson (24) have reviewed gastrointestinal cell proliferation and differentiation and regulation of gastrointestinal growth, but the specific roles of diet composition and level of intake are not well defined.

The positive correlation between visceral organ mass and fasting heat production (13, 14) would suggest that any nutritional regimen which increases relative mass of visceral organs may result in higher oxygen consumption and metabolic rate of those organs.

The increased energy costs of maintenance (1066 kcal ME $kg^{-.75}$) and protein deposition (157 kcal ME g^{-1}) of pregnant gilts (4, 5) is associated with an additional metabolic adaptation to satisfy the needs of the gravid uterus and developing fetuses. There appears to be no anabolic effect of pregnancy in primiparous gilts other than the increased growth of reproductive and mammary tissues (4, 5, 25–27). The increased relative weight of the reproductive tract of feed restricted (R) gilts in the present experiment compared to that of gilts fed adequately (C), in the absence of a change in the relative weight of trimmed lean tissue, supports this concept. However, the reproductive tract of gilts restricted only in carbohydrate and fat calories (RCal), whose relative stomach and kidney weights were greater than those of R and C gilts, failed to show a pregnancy anabolic response of a magnitude equal to that of R and C gilts. Weight of the empty uterus, excluding fetuses, was significantly less in RCal than in R and C gilts. Total uterus (including or excluding fetuses and fluids) plus gastrointestinal tract weight was also less in

RCal than in R or C gilts when expressed in absolute terms (kg), but when expressed as relative weight (percentage of body weight), the values were higher for R than for RCal and C gilts. The data support the concept of differential responses of the reproductive tract related to nutritional regimens that affect kidney and visceral organ mass. The results are interpreted to indicate that the apparent effect of the high-protein, low-carbohydrate and -fat-calorie diet on relative weight of kidney and stomach observed in this experiment and previously (11) and the associated increase in fasting heat production (13, 14) provide less energy available for reproductive tissue accretion. The lower backfat depth and other indices of body fatness and lower body weight at slaughter at Week 15 of gestation in RCal than in R and C gilts support the conclusion that less energy was available for maintenance of body weight and body fat reserves in RCal than in R gilts.

The higher plasma glucose and plasma urea-N concentrations of RCal gilts than of R and C gilts denote metabolic adaptations related to diet energy and protein intakes. The higher plasma glucose is suggestive of a diabetogenic effect of the high-protein–low-carbohydrate diet. This tendency was reflected in the higher plasma-glucose in fetuses of RCal gilts than that of other gilts. Fetal tissue glycogen stores and plasma glucose are generally considered to be refractory to maternal energy intake in swine (28–30); induction of maternal alloxan diabetes does increase fetal glycogen reserves (31). The elevation of plasma glucose in fetuses from RCal gilts in the present experiment was not associated with a change in fetal weight; fetal tissue glycogen content was not measured. The elevated plasma urea-N in RCal gilts and their fetuses probably reflected deamination of dietary protein for gluconeogenesis in the presence of inadequate energy intake. Urea-N is readily transported from maternal plasma to the fetus and probably accounts for the higher plasma concentration of urea-N in fetuses from RCal dams than in those from other dams.

Plasma protein tended to be lower ($P < 0.07$) in R than in RCal and C dams and plasma albumin was less ($P < 0.03$; R < RCal = C), confirming the suboptimum daily protein intake expected in gilts restricted to one-third of the (21) recommended level of gestation diet. The degree of protein inadequacy was not sufficient to cause a reduction in maternal or fetal hematocrit or in fetal plasma total protein or albumin in the R group compared with values recorded for the RCal group. However, fetal plasma total protein was less in fetuses from R dams than in fetuses from C dams. Plasma albumin in 108-day fetuses was reduced significantly by maternal feed restriction in previous work (1) in which fetal weight was depressed to a degree similar to that observed in the present experiment.

We conclude that severe restriction of carbohydrate and fat calories only, compared with severe restriction of a standard diet throughout gestation in swine, has a negative effect on uterine growth. This effect is associated with increased kidney and stomach relative weights and suggests increased kidney, visceral organ, and lean tissue maintenance costs at the expense of maternal uterine tissue and body fat conservation. This phenomenon has important implications for the responses of humans to certain weight reduction regimens in which prescribed diets are extremely high in protein, vitamins, and minerals but restricted in fat–carbohydrate calories.

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