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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XLVI. Relation Between Heat Increment of Gestation and Birth Weight

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COLUMBIA, MISSOURI

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FOREWORD

The special investigation on growth and development is a cooperative enterprise in which the departments of Animal Husbandry, Dairy Husbandry, Agricultural Chemistry, and Poultry Husbandry have each contributed a substantial part. The parts for the investigation in the beginning were inaugurated by a committee including A. C. Ragsdale, E. A. Trowbridge, H. L. Kempster, A. G. Hogan, F. B. Mumford. Samuel Brody served as Chairman of this committee and has been chiefly responsible for the execution of the plans, interpretation of results and the preparation of the publications resulting from this enterprise.

The investigation has been made possible through a grant by the Herman Frasch Foundation, now represented by Dr. F. J. Sievers.

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ABSTRACT

1. The amount of extra heat produced, Q, during gestation above the non-gestation level (at rest) is related to the birth weight, M, of the offspring (of different species from rats to horses) by the equation $Q = aM^n$. The numerical value of n is of the order of 1.2, and of a is 4400; which means that the formation of a fetus of 1 Kg. at birth is associated with a heat increment of gestation of 4400 Calories, and when the birth weight is not 1 Kg, the heat increment appears to vary with the 1.2 power of birth weight. *2.* This heat increment of gestation—4400 Cal. for a 1-Kg. offspring at birth—differs by less than 10% from the Rubner constant of 4808 Cal.—"the amount of energy which is necessary to double the weight of the newborn." *3.* The surface law is not applicable to prenatal growth.

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XLVI. Relation Between Heat Increment of Gestation and Birth Weight

SAMUEL BRODY

I. DEFINITION AND AIM

The literature on energy metabolism during gestation, reviewed briefly in the preceding paper,[1] is concerned with the following aspects: 1. The time course of heat production with the advance of gestation; 2. The reference units for heat production. Should the heat production during gestation be expressed with reference to: (a) total body weight, (b) surface area of gestating animal, or (c) sum of separate surface areas of mother and of fetus? 3. The mechanisms that increase resting heat production during gestation. Is the increased metabolism during gestation the result of: (a) increased endocrine activities, particularly the pituitary-thyroid complex, (b) metabolism of fetus, or (c) increased metabolism of mother as result of supporting the pregnant uterus? This literature on the metabolism of gestation is thus concerned with the qualitative and semi-quantitative aspects of metabolism.

The present bulletin, on the other hand, is concerned not with the qualitative, but with the quantitative aspects of the metabolic level during gestation. The purpose of this paper is to present and generalize data on the *amount* of extra heat produced (during rest) as result of gestation, and the relation of this *gestation heat increment* to the birth weight of the offspring in different species.

II. THE RELATION BETWEEN HEAT INCREMENT OF GESTATION (OR INCUBATION) AND BIRTH WEIGHT OF OFFSPRING

The method for evaluating the heat increments of gestation is detailed in the next section. This section is concerned with the interrelation between heat increment of gestation and newborn weight. This relation is presented graphically in Fig. 1 based on data in Table 1. Most of the metabolism data discussed in this bulletin were previously published in other connections in Missouri

[1]Brody, S., Riggs, J., Kaufman, K., and Herring, V. Energy metabolism levels during gestation, lactation, and post-lactation rest. Univ. Missouri Agr. Exp. Sta. Res. Bul. 281, 1938.

PAPER 168 IN THE HERMAN FRASCH FOUNDATION SERIES.

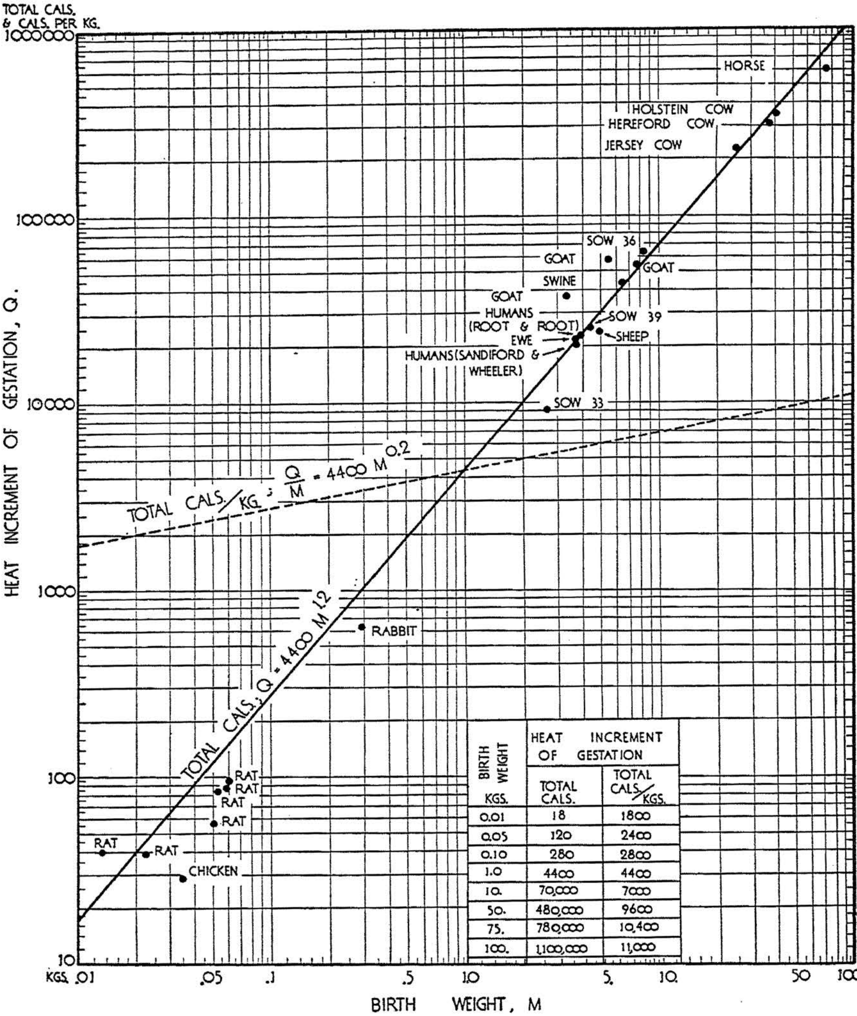


Fig. 1.—The relation between the heat increment of gestation, Q, and birth weight, M, of the offspring plotted on a logarithmic grid. The broken curve and solid circles represent the ratios of the heat increments of gestation, to birth weight of young; the continuous heavy curve and crosses represent the total heat increment of gestation plotted against birth weight.

Research Bulletins 166, 176, and 281, to which the reader is referred for further information.

Fig. 1 shows that if the total heat increment of gestation (that is the heat production of gestating animal above the heat production of the same animal when not gestating) is plotted against newborn weight on a logarithmically divided grid, the distribution of

TABLE 1. DATA ON THE RELATION BETWEEN THE HEAT INCREMENT OF GESTATION AND BIRTH WEIGHT OF OFFSPRING

Species & Breed	No. of Animals in Average	Weight of newborn Individual or litter Kgs.	Estimated Surface Area of newborn Sq. meters	Mother's Wt. gain during pregnancy Kg.	Heat Increment of Gestation		Gestation Period Days	No. in Litter	Source
					Total Cal.	Cal./kg. Birth Wt.			
Percheron Horse	1	74.0	1.505	113	591,000	7986	340	1	Original
Holstein Cows	16	40.8	1.197	94	353,400	8662	283	1	"
Hereford Cows	3	31.8	1.040	45	304,500	9575	283	1	"
Jersey Cows	18	25.4	.918	44	228,300	8988	283	1	"
Duroc-Jersey Swine ..	6	6.5	.....	9	42,120	6480	114	..	"
Duroc-Jersey Swine ..	1	8.1	.....	10	65,520	8089	114	7	"
Duroc-Jersey Swine ..	1	4.3	.....	.....	25,500	5930	114	3	"
Duroc-Jersey Swine ..	1	2.7	.....	6	9,200	3407	114	2	"
Dorset Sheep	1	5.0	.300	6	23,800	4755	150	1	"
Dorset Sheep	1	3.7	.251	5.5	21,600	5838	150	1	"
Human	1	3.8	.251	8.3	22,540	5932	280	1	Root & Root
Human	1	3.6	.242	7.7	21,805	6057	280	1	Sandiford & Wheeler
Goat	1	7.7	.455	1.5	53,300	6922	150	2	Original
Goat	1	3.2*	.203	—1.8	37,300	11660	150	1	"
Goat	1	5.2*	.347	3.2	57,800	11120	150	2	"
Rat	1	0.0225	.....	.....	38.7	1724	21	5	Original
Rat	1	0.0135	.....	.....	38.8	2874	21	3	"
Rat	1	0.058	.....	0.016	88.3	1522	21	12	"
Rat	1	0.050	.....	0.014	57.0	1140	21	9	"
Rat	1	0.059	.....	0.024	94.8	1607	21	13	"
Rat	1	0.052	.....	0.026	84.8	1631	21	12	"
Domestic Fowl**	.	.....	.116	.....	19	501	21	..	Average various sources

*Estimated on basis of average values.
**Omitted from correlation.

the data assumes a linear form. The equation in Fig. 1 was fitted to the data (weighted averages and individual data) by the method of least squares. The intercept of the curve is 4400, and the slope of the distribution line is 1.2. This means that the production of an offspring (or litter) weighing 1 Kg. at birth tends to be associated with a gestation heat increment of about 4400 Calories. The magnitude of this heat increment changes with the 1.2 power of the weight of the offspring. This means that the logarithmic (or relative) increase in the heat increment of gestation tends to be 1.2 times the logarithmic (or relative) increase in birth weight of offspring. In other words increasing birth weight by 100% tends to increase the heat increment of gestation not by 100%, but by somewhat over[2] 120%.

It is interesting and perhaps significant that the heat increment of gestation of 4400 Cal. for a 1-Kg. newborn differs by less than 10% from the Rubner constant of 4808 Cal.—"the amount of energy which is necessary to double the weight of the newborn." Our equation of course differs from "Rubner's law of growth" in that Rubner's law is concerned with the total energy (including that stored in the body) during the doubling of birth weight, while our equation is concerned with the extra heat produced by the mother as result of gestation; and this extra heat production does not include the energy stored in the body of the fetus.

If instead of absolute total heat increment of gestation we plot total heat increment per unit weight of newborn against weight of newborn, then Fig. 1 shows that the slope of the resulting representative straight line is 0.20. This means that increasing newborn weight by 100% tends to be associated with an increase in heat increment of gestation per unit newborn weight by somewhat above 20%.

The obvious and "practical" interests of Fig. 1 are: (a) it presents a generalization of a large body of data by a mathematically simple formula and pictorially compact chart; (b) it presents a beginning towards estimating the energy cost of prenatal growth without reference to species. This generalization may perhaps be termed a "law" of constant energy expenditure during prenatal

[2]The 1.2 value of the exponent in the equation in Fig. 1 is convertible directly to percentages only if the change in the independent variable is very slight. Thus in the equation $Q = M^{1.2}$, $\frac{dQ}{Q} = 1.2 \frac{dM}{M}$, where dM is a very small change in birth weight M. As the value of dM increases, the value of the exponent is increased above the 1.2 value. Increasing birth weight, M, by 100% changes the value of the exponent from 1.2 to 1.3; that is, increasing M by 100% increases Q not by 120% but by 130%; increasing M 1000% increases Q not 1020% but 1570%. In other words, the exponent 1.2 is the lowest limiting value when the independent variable is increased by an infinitessimally small increment. But for finite increments the relative changes in the dependent variable is always greater than that indicated by the value of the exponent.

growth in the same sense that Rubner's relation of energy cost for doubling birth weight is called a law.

The gestation heat increment, that is, the energy dissipated for producing the newborn, includes: (1) energy expense of maintenance of the pregnant uterus; (2) "work" of converting non-living growth precursors in maternal blood to the living organism of the new animal; (3) increased work of the maternal organism (increased circulatory, respiratory, and excretory activities) associated with gestation. (4) It no doubt includes other factors, such as the effects of endocrinal influence on metabolism. The preceding report[1] reviewed briefly the literature on the evidence for increased endocrine activity—especially pituitary and thyroid—during gestation. Because of these complications, it does not seem practical to attempt to interpret at this time the theoretical significance of the numerical interrelations presented in Fig. 1. The present paper is confined to the presentation of the factual material as we have it.

III. GESTATION HEAT-INCREMENT DATA

The reliability of the generalization in Fig. 1 is no greater than the constituent data on which it is based. It therefore seems proper to discuss the character of the constituent data.

1. Domestic Fowl.—The heat production during incubation of the chick embryo (domestic fowl) is plotted in Fig. 2. It is seen to be of the order of 19 Cal. (19040 cal.). The heat production of the chick during incubation, is of course also the heat increment of incubation or "gestation".

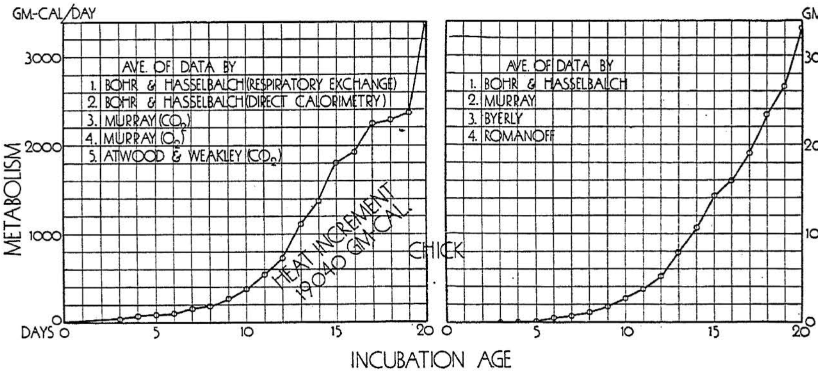


Fig. 2.—The time curves of heat production and embryo weight of the incubating chick, and the heat increment (total heat produced during incubation) of incubation. Sources of data indicated on chart. For references see Mo. Ag. Exp. Sta. Res. Bul. 96, 1926.

In comparison to the general curve in Fig. 1, the heat production associated with incubation in the chick is rather low. This accords with expectations. While the heat production in the incubating chick is of course distinct from that of its mother, the heat increment of gestation in mammals includes the influences of the various gestation effects (outlined in preceding section) on the mother's heat production. The reader may indeed object—in part rightly—to the combination of the data on heat increment of incubation of birds with the heat increment of gestation data of mammals.[3] On the other hand the difference between the heat production of the chick embryo and the general curve of the heat increment of gestation may be of interest in helping to differentiate between the heat production of the embryo or fetus proper, and the effect of gestation on the heat production of the mother.

2. Cattle.—It is not practicable to secure gestation-metabolism data on dairy cattle distinct from heat production of growth or/and of milk production of the mother. Cattle are generally first bred at the age of about 20 months when they are still growing rapidly, and gestation is thus complicated by growth. Cattle are then bred in the early period of lactation, so that the heat increment of gestation is masked by the heat increment of lactation which, as previously explained, is very high.

The data on the heat increment of gestation presented in Fig. 3 were obtained on cattle during their first gestation period when they were still growing rapidly.

The *heavy curves* in Fig. 3 represent the observed heat production (left) and body weights (right). The heat production was measured by the O_2-consumption method, while the animals were lying at rest, about 12 hours after the preceding evening's feeding.[4] The *light curves* represent the estimated weights and metabolism as they would be if the animals were not pregnant. The area between the heavy and light metabolism curves represent the heat increments of gestation.

Fig. 3 shows that, employing this method, the heat increments of gestation are: 353,400 Cal. for the Holstein cows; 228,300 Cal. for the Jersey cows; 304,500 Cal. for the Hereford cows.

The above values for the heat increments of gestation of these several breeds of cattle parallel the respective live weights of the animals (see Table 1).

Fig. 1 shows that the cattle data are close to the general line relating gestation heat-increment and newborn weights for the first

[3]The equation in Fig. 1 does not include the chick data.
[4]See Missouri Res. Bul. 143 for method of measuring metabolism of these animals.

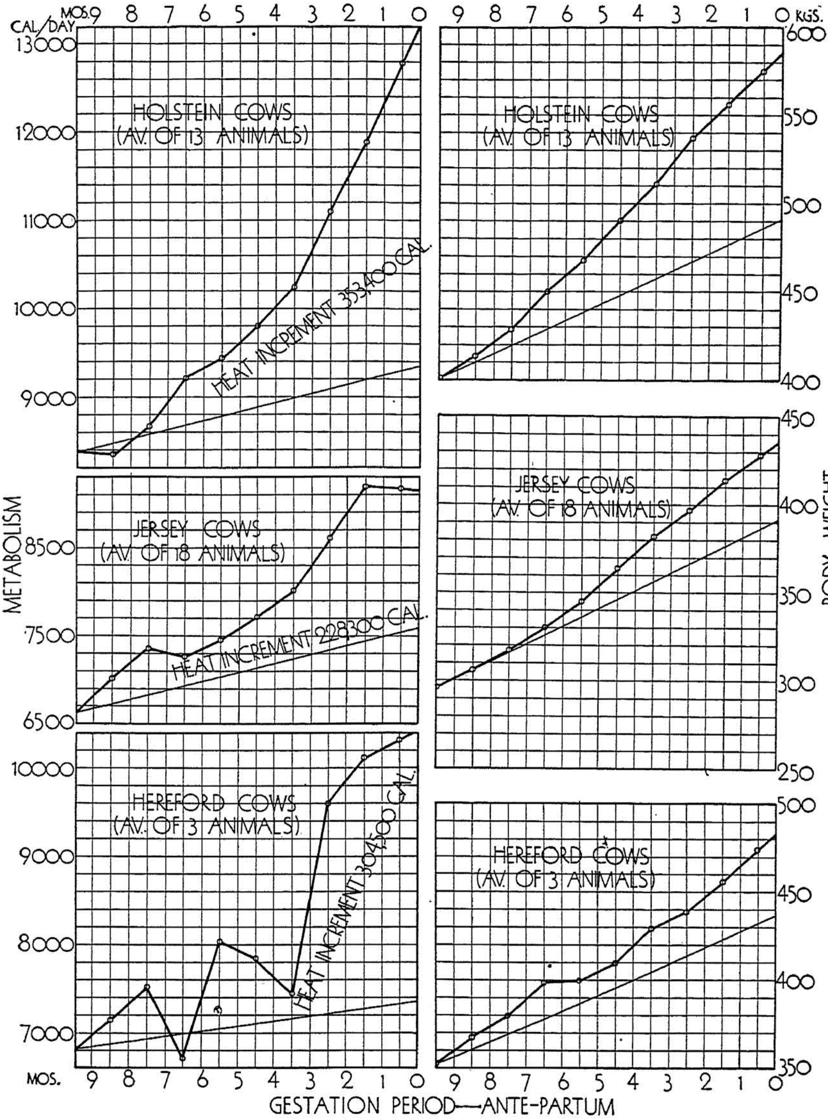


Fig. 3.—The time courses of heat production (left) and live weight (right) with the advance of the period of gestation in cattle. The heavy curves represent the observed values; the light curves represent non-gestating "normals" of the same age. The area between the heavy and light heat-production curves represent the heat increments of gestation.

gestation period.

3. Horses.—The data for the resting metabolism of a rather large horse are presented in Fig. 4.

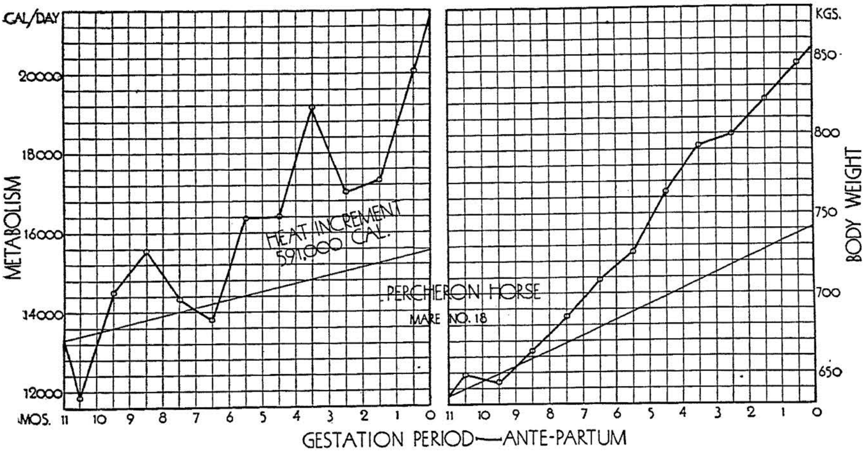


Fig. 4.—The time course of heat production (left) and live weight (right) with the advance of the period of gestation in a horse. See legend to Fig. 3 for additional comments.

The distribution of data is somewhat irregular. The gestating animal was growing rapidly herself as indicated by the slope of the light lines representing the assumed course of weight and metabolism that she would exhibit if she were not pregnant. However, the gestation heat increment, 591,000 Cal., representing the space between the light and heavy metabolism curve, is very reasonable, and is seen to be quite close to the average line in Fig. 1.

4. Swine.—The time curves of body weight and resting metabolism of immature hogs are shown in Fig. 5. As before, the light lines represent the assumed course of weights and metabolism of the animals if they were not pregnant. The heat increments of gestation correspond to the areas between the light and heavy lines.

The gestation heat increments depend on the number of pigs in the litter, and therefore on the litter weight. With the exception of sow 33, the data come quite close to the average line.

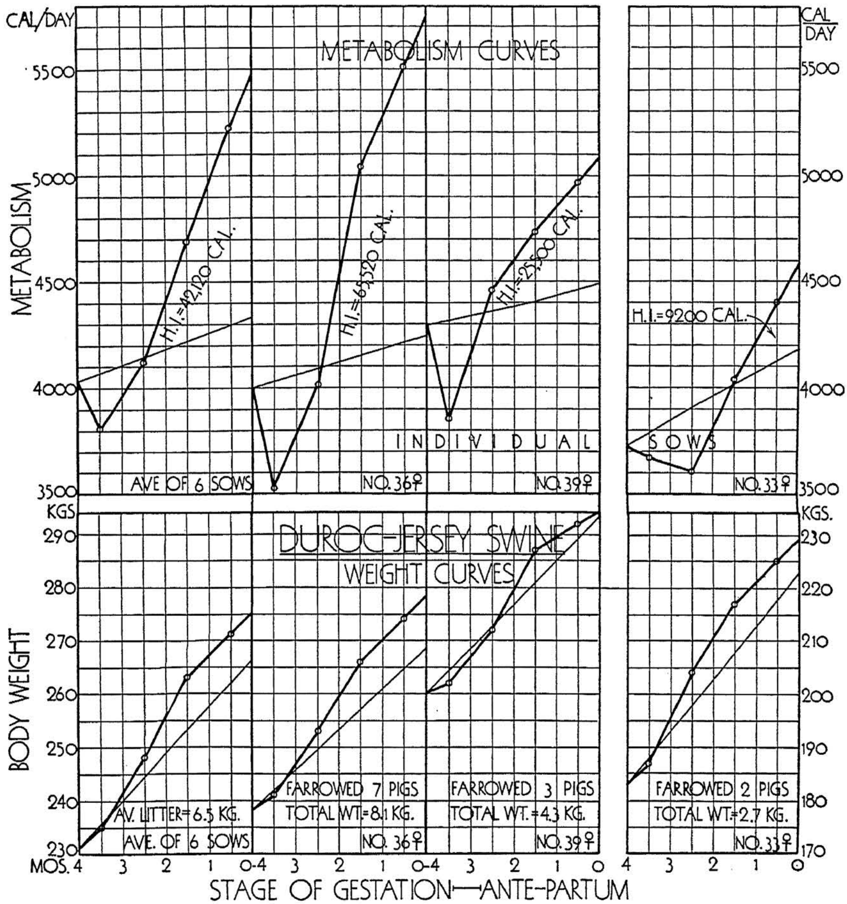


Fig. 5.—Time curves of heat production and live weight of gestating swine. The numbers of pigs in the litters, and the litter weights are indicated at the bottom of the chart. Note variations of the H. I. (heat increments) with litter size. See legend to Fig. 3 for additional explanations.

5. Sheep.—Fig. 6 presents our data for the gestating heat increment of sheep, which is of the order of 23,000 Calories. The sheep data are satisfactorily close to the general line in Fig. 1,

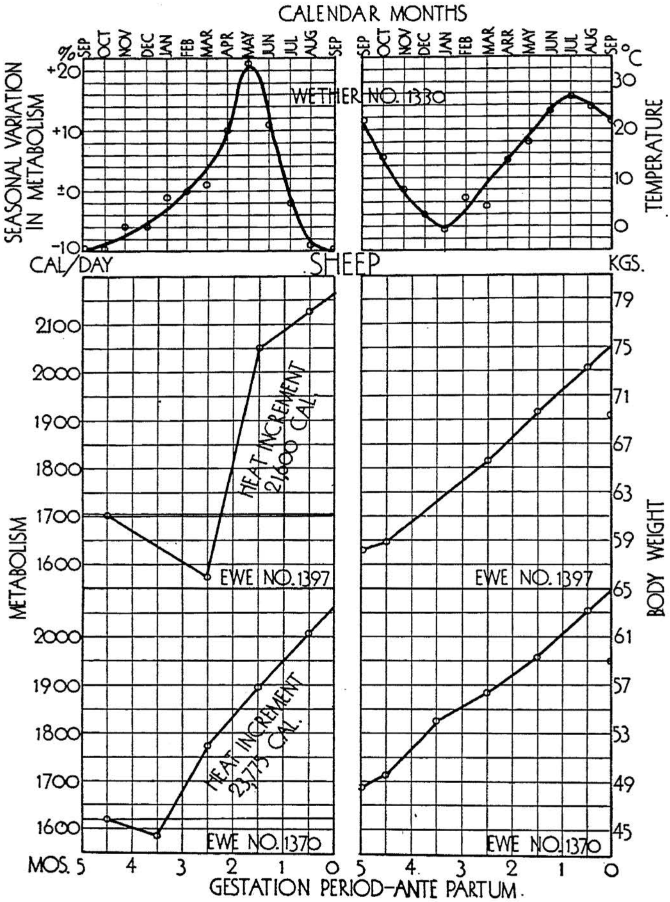


Fig. 6.—Time curves of heat production and body weight of gestating sheep. See Fig. 3 for further explanations. The upper left curve indicates a complication in computing the heat increment of gestation: There is a seasonal metabolic rhythm (shown on a castrated male) which had to be corrected for. The upper right curve represents seasonal variations in environmental temperature.

The upper left curve in Fig. 6 indicates the presence of a seasonal metabolic rhythm in a castrated (wether) sheep, i.e., a metabolic rhythm independent of sex function. The curve on the upper right represents the temperature rhythm in Columbia, placed here to suggest a possible relation between temperature (which is associated with amount of light) and metabolic rate.

6. **Goat.**—Fig. 7 presents our data for the gestation heat increment of goats, which is of the order of 50,000 Calories. The goats were heavier than the sheep, but we did not expect that the gestation heat increment of the goats would be so much greater than of the sheep. Two of the goat values are quite a distance from the average line in Fig. 1.

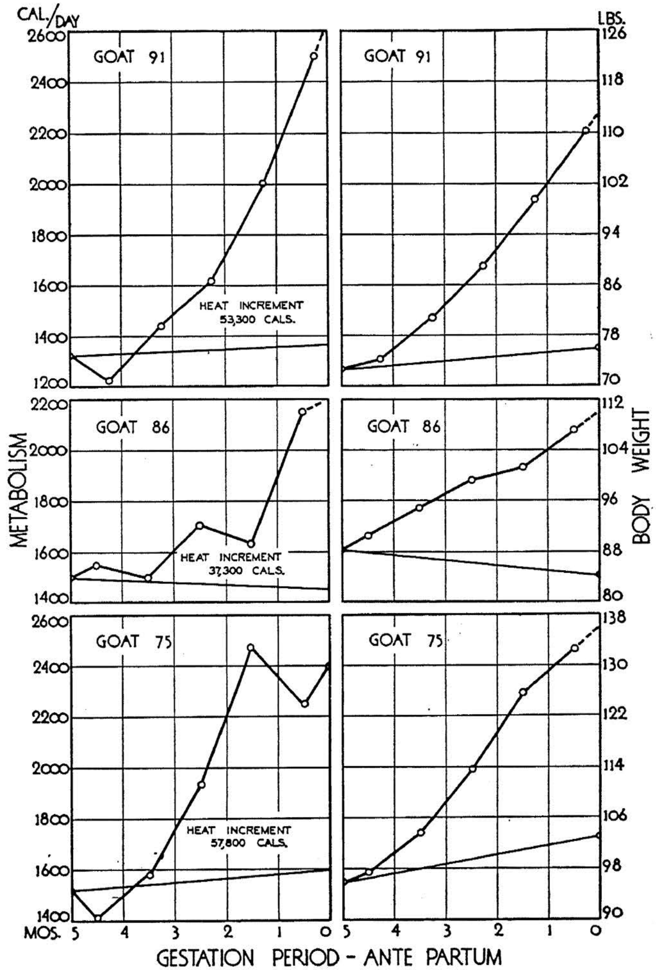


Fig. 7.—Time curves of heat production and body weight in gestating goats. See legend to Fig. 3 for additional comment.

7. **Rats.**—Fig. 8 presents our data for the gestation heat increments of rats, which range from 39 to 94 Calories depending on litter size and other factors. These curves are based on data published in the preceding paper of this series (Missouri Res. Bul. 281). With one exception, the heat increment of gestation in the rat is considerably below the average line in Fig. 1.

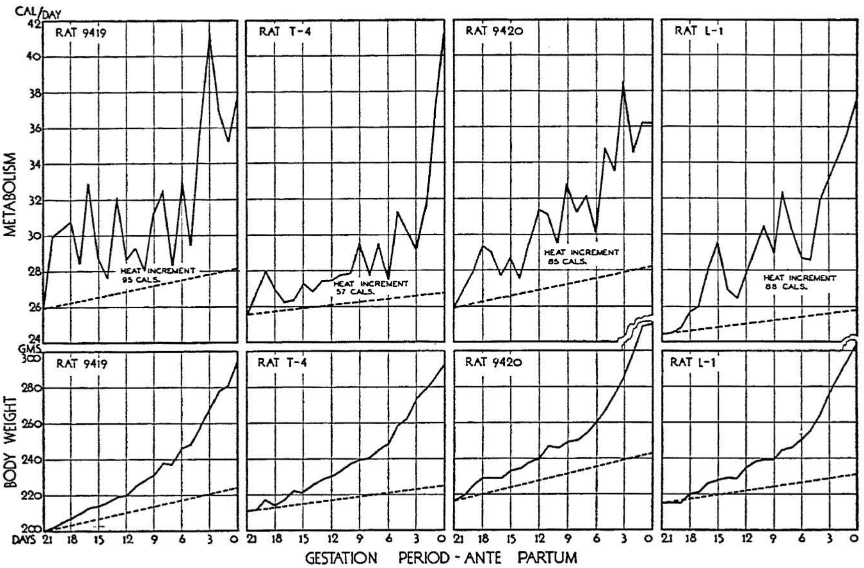


Fig. 8.—Time curves of heat production and body weight in gestating rats. See Fig. 3 for additional explanations. Broken curves represent non-gestating levels.

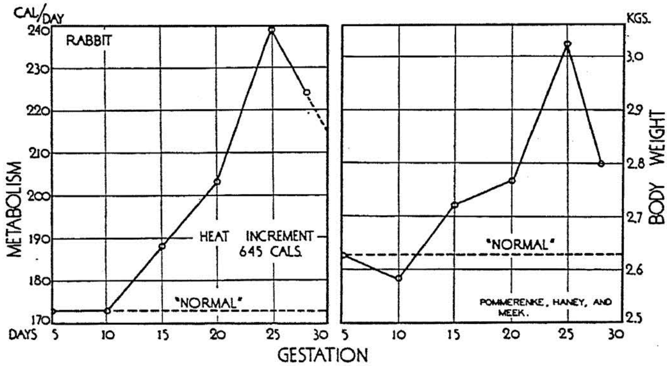


Fig. 9.—Time curves of heat production and body weight in the gestating rabbit. See Fig. 3 for additional comments. This chart was prepared in part from data published by Pommerenke, Haney, and Meek in Am. J. Physiol., *93*, 249, 1930, and in part from unpublished data sent us by these authors.

8. Rabbit.—Fig. 9 shows that the heat increment of gestation in the rabbit is of the order of 645 Calories. Fig. 1 shows that the rabbit heat increment datum is below the general curve. The data are not adequate for deciding whether or not the deviation is within the limits of experimental error. It appears, however, that the less mature the species at birth the lower the heat increments of gestation in comparison to the average curve in Fig. 1.

9. Humans.—Fig. 10 indicates that the heat increment of gestation in humans is of the order of 23,000 Calories, the same as in

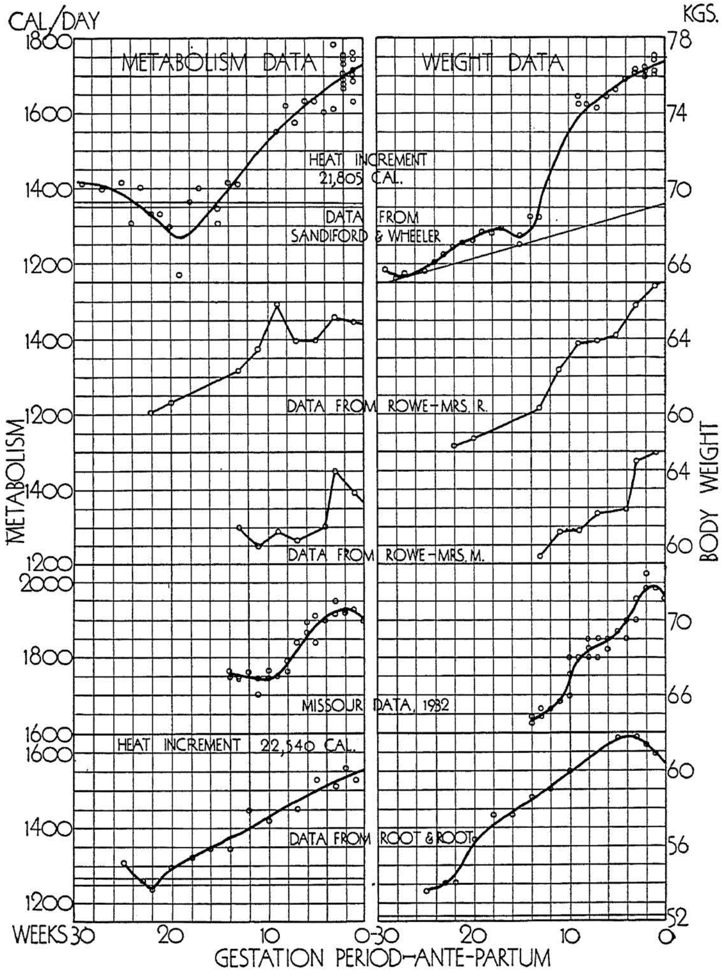


Fig 10.—Time curves of heat production and body weight in gestating humans. See Fig. 3 for additional explanations.

sheep, which does not seem reasonable in view of the differences in maturity at birth in the two species. We suspect that our heat increments of gestation in sheep are for some reason too low.

10. Note on a Decline in Metabolism in Early Gestation.—Most of the preceding time curves of gestation exhibit a slight metabolic decline in the early period of gestation. Benedict and Ritzman, and Ritzman and Benedict[5] report a decline in heat production in early gestation of sheep, and no increase in gestation metabolism when expressed with respect to unit area or unit weight. The German article reports:

> "Graviditat keinen ausgesprochenen Einfluss auf die Wärmeproduktion der Schafe pro kilogramm korpergewicht oder pro Quadrameter Oberflache ausübt."

The N. H. bulletin reports:

> "The heat production is the same on the surface area basis, although the weight basis shows a lower tendency during the first month of gestation.
>
> "There is, thus, a very strong suggestion that the drop in metabolism may have some connection with pregnancy. The general trend indicates a gradual lowering in metabolism from the first to the third month of pregnancy after which it increases again, slowly at first, but with a very decided rise at about a month before lambing.
>
> "If the decline during the first three months of gestation is thus the direct result of pregnancy, which is suggested but not definitely established by these data, then the sheep behave contrary to what has been found to be the case with humans and with the goat."

However, Rowe and Boyd[6] reported a similar decline in humans.

> "During the 3rd to 4th month of gestation there is a rapid decline in the energy requirement from a normal to a subnormal level, the latter reach in about 4 weeks. From this point on, during the last 6 lunar months there is a steady increase in the basal metabolic rate."

[5]Benedict and Ritzman, Arch. Tierernahrung und Tierzucht, Abt. B. 5, 41, 1931; Ritzman and Benedict, Tech. Bul. 45, New Hampshire Agr. Exp. Station 1931.

[6]Rowe, A. W., and Boyd, W. C., The metabolism in pregnancy, J. Nutrition, 5, 551, 1932.

IV. RELATION BETWEEN THE COURSE OF HEAT INCREMENT OF GESTATION OR INCUBATION AND THE COURSE OF FETAL SIZE (SURFACE AREA AND WEIGHT)

1. Introduction and Notes on Fetal Metabolism.—Rubner believed that his "surface law" as it relates to heat production is applicable to prenatal and to postnatal life. In the preceding bulletin[1] we reviewed papers by Murlin and Carpenter; Sandiford and Wheeler; Pommerenke, Haney and Meek; which appear to substantiate Rubner's belief; and papers by Rowe et al., and Schwarz and Drabkin, which seem to oppose Rubner's belief. The view of Barcroft,[7] the most distinguished contemporary investigator of fetal metabolism, is indicated by the following free quotations.

> The fetus has no cooling surface and is under no necessity to keep up its own body temperature. . . . That the metabolism of the fetus is much reduced is evident from its flaccid condition.

It is generally known that there is an intimate interrelation between circulatory and respiratory functions. Barcroft's ideas concerning the interrelation between blood volume and fetal surface and weight are therefore cogent in this place:

> It is usual to express blood volume either as a percentage of the weight of tissue through which the blood circulates, or as a function of the surface area of the body. Both of these conventions in the case of the fetus present difficulties. The embryo has no surface, if the word surface be used in the physiological sense, intended to convey to the reader the idea of an area from which heat is dissipated. There seems little point therefore in calculating the relation of the blood volume to the cutaneous area. As regards the blood volume considered in relation to body weight, two possibilities exist. The body weight in the case of the fetus is not the same thing as the weight of material through which circulation takes place, unless indeed the placenta be regarded as an integral part of the fetus. We may therefore calculate the fetal blood volume as a percentage of the weight of the actual embryo or as a percentage of that of the embryo plus the placenta.

As pointed out in 1928,* the heat production in the chick embryo varies not with surface area ($\frac{2}{3}$ power of body weight), but with the 0.5 power of body weight between weight range 0.1 to 2.0 gm; 1st power between 2 and 20 gm; 0.5 power between 20 gm. and hatching (35-40 gm). This changing power relation with increasing body weight is also demonstrated in Fig. 1 of the immediately preceding report of this series.[1]

Barcroft represented oxygen consumption in the fetal sheep, and blood volume in the fetal goat, as percentage of the fetal weights. It may be instructive to compute the power-function interrelation between metabolism and fetal body weight for Barcroft's

[7]Barcroft, J., Fetal circulation and respiration. Physiol. Rev. *16*, 103, 1936.
*Missouri Agr. Exp. Sta. Res. Bul. 115, 1928, p. 53.

fetal sheep data, as we previously did for the chick data, by plotting metabolism and blood volume against weight on logarithmic coordinate paper, and fitting the equation $Y = aX^n$ to the data. This was done with results shown in Fig. 11, based on Barcroft's data.

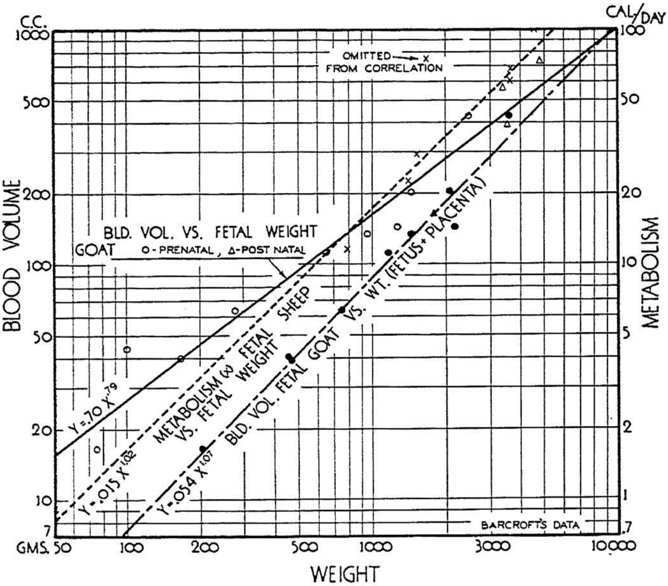


Fig. 11.—Interrelation between blood volume, metabolism, and fetal weight in goats and sheep, plotted from data by Barcroft et al.

Fig. 11 shows that the fetal metabolism in the sheep increases directly (1.0 power) with body weight. The blood volume in the fetal goat increases with the 0.79 power of fetal weight, and with the 1.0 power of the combined weight of fetus and placenta. Several other curves shown in Fig. 11 may have some interest in this connection.

It is difficult to interpret these results except to say that the data do not furnish evidence in favor of the applicability of the "surface law" to prenatal metabolism. The facts that the fetus is only a part of the pregnant uterus (See Fig. 12), and a still smaller part of the total weight gain during gestation, and that gestation is associated with changes in endocrine activities, makes it extremely hazardous to defend the applicability of the "surface law" to prenatal life.

Nonetheless, since this paper is devoted to the gestation heat increments of different species it will be instructive to examine the data from the viewpoint of the relation of heat increment to size of embryo or fetus.

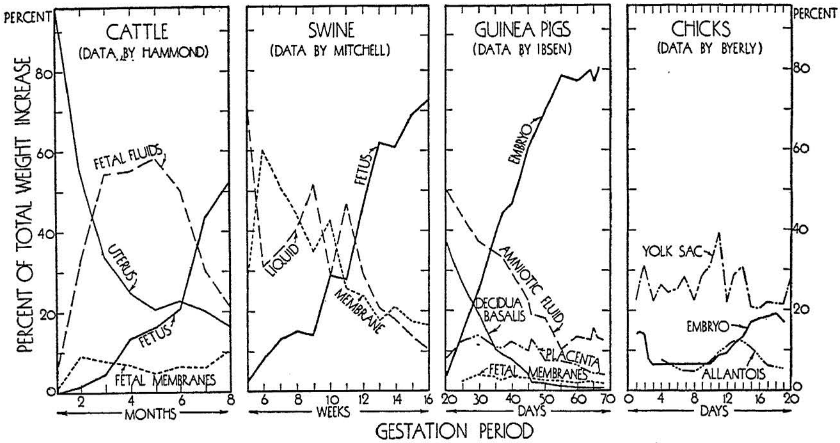


Fig. 12.—The time course of distribution of weight increases between embryo or fetus and adnexa to illustrate the fact that the fetus is only a part of the total weight gains of the pregnant uterus during gestation.

In the following discussions, with one or two exceptions specifically noted, the heat production data are original, obtained in this Station (see Missouri Res. Buls. 166, 176, and 281), while the data for fetal weights and adnexa were taken from the literature by authors indicated on the respective charts.

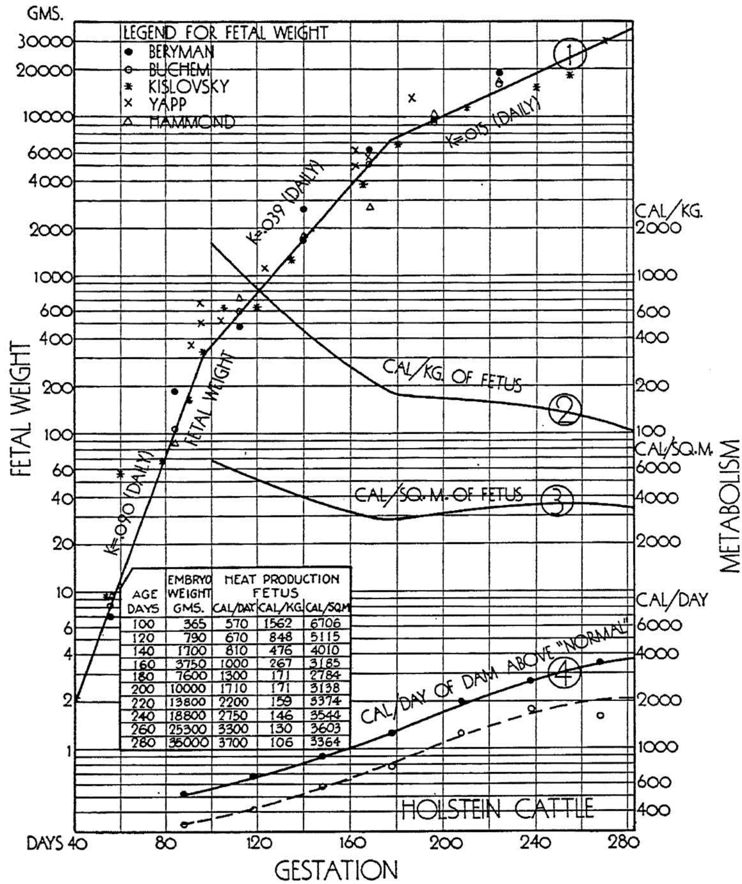
2. Cattle.—Curve (1) in Fig. 13 represents fetal growth. The k-values represent slopes (relative changes, or percentages when multiplied by 100) on this arithlog grid. Thus when $k = 0.09$, the slope, or *relative growth rate*, is 0.09, or *percentage growth rate* is 9% per day or 270% per month and so on.

The reason for plotting the data on an arithlog grid is that the slopes of the curves represent relative or percentage changes regardless of the abolute units employed. Thus, if the time curves of growth in weight and increase in metabolism are parallel, then the percentage changes in the two processes are the same; if the weight curve is twice as steep as the metabolism curve, then the percentage increase in weight is double that of the metabolism.

Curve (4) represents the course of metabolism due to pregnancy. It represents total metabolism less the computed "normal" metabolism assuming that the animals were not pregnant.

Curve (2) represents the extra metabolism (4 above) divided by the corresponding fetal weights.

Curve (3) represents in similar manner extra metabolism per square meter of fetus. The area of the fetus was computed from



AGE DAYS	EMBRYO WEIGHT GMS.	HEAT PRODUCTION FETUS CAL/DAY	CAL/KG	CAL/SQ.M
100	365	570	1562	6706
120	790	670	848	5115
140	1700	810	476	4010
160	3750	1000	267	3185
180	7600	1300	171	2784
200	10000	1710	171	3138
220	13800	2200	159	3374
240	18800	2750	146	3544
260	25300	3300	130	3603
280	35000	3700	106	3364

Fig. 13.—A comparison on an arithlog grid of the time curves of: (1) fetal weight; (2) Calories of excess metabolism above "normal" per kilo of fetus; (3) Calories excess metabolism above normal per square meter of fetus; (4) Calories per day of pregnant cow above the non-pregnant level. Curves (2), (3), and (4) were computed with respect to the Holstein cattle; the lower broken curve represents Jersey cattle.

the formula.*

$$\text{Area} = 0.15\ W^{.56}$$

Curves (2) and (3) do not represent respectively the metabolism per kilo and per square meter of fetus, but the *extra* metabolism (above what it would be if the animals were not pregnant) per unit weight and per unit area of the fetus. These values are evidently too high to represent the metabolism of the fetus, and therefore oppose the conclusion of Sandiford and Wheeler that the heat

*Cf., Missouri Res. Bul. 115.

increment of pregnancy may be accounted for completely by the metabolism of the fetus.

3. Humans.—Fig. 14 presents a similar chart for humans. The curve on the left, with its scale of ordinates on the left side, represents fetal weights. The curves on the right, with their ordinate

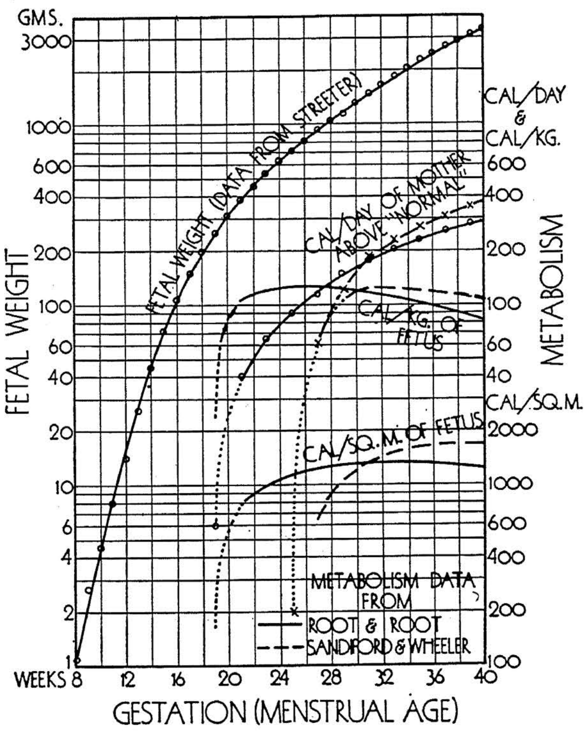


Fig. 14.—Continuation of Fig. 13, but as regards human.

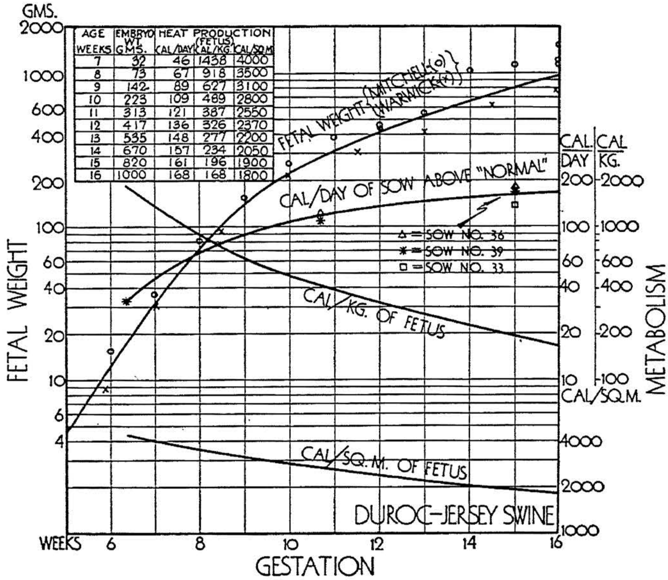
scales on the right, represent the heat increments of gestation in various ways: total per day; per kilo fetal weight; per sq. meter fetal surface. The surface area of the fetus was computed from the formula*

$$\text{Area} = 0.10\ M^{0.69}$$

The remarks in the preceding section concerning cattle apply to the curves for humans. The heat production per unit weight and per unit area is too high to represent the heat production of the fetus alone. It undoubtedly includes an extra heat production of organs concerned in the nutrition and protection of the fetus, and extra heat production of the maternal organism under the influence of pregnancy (endocrine activity), as discussed in the review of literature of the preceding bulletin.[1]

4. **Swine.**—Fig. 15 represents similar data for swine, employing our data for heat increment, and fetal-weight data by Mitchell and by Warwick. The fetal surface was computed from the formula*

$$\text{Area} = 0.097\ M^{0.633}$$



AGE WEEKS	EMBRYO WT. GMS.	HEAT PRODUCTION (FETUS) CAL/DAY	CAL/KG.	CAL/SQ.M.
7	32	46	1438	4000
8	73	67	918	3500
9	142	89	627	3100
10	223	109	489	2800
11	313	121	387	2550
12	417	136	326	2370
13	535	148	277	2200
14	670	157	234	2050
15	820	161	196	1900
16	1000	168	168	1800

Fig. 15.—Continuation of Fig. 13, but as regards swine.

5. Sheep.—Fig. 16 represents data for sheep.

The fetal age curve of the sheep represented by circles and continuous line is based on unpublished data by our colleague, Dr. Fred McKenzie. The age curve is represented by crosses, and broken curve is based on data by Barcroft and associates (which were not used for relating the heat increment of gestation). The surface area of the fetal sheep was computed from the formula*

$$\text{Area} = 0.125\ M^{0.57}$$

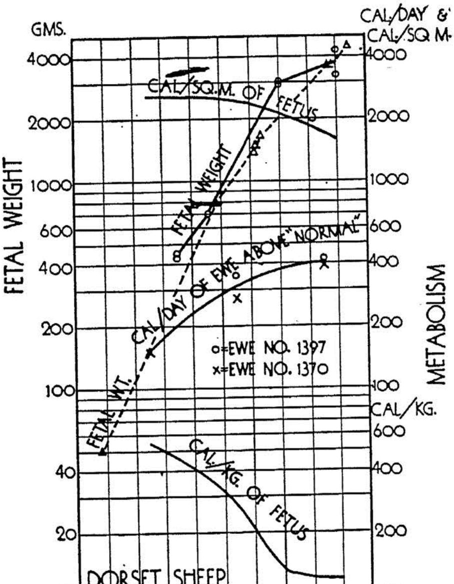


Fig. 16.—Continuation of Fig. 13, but as regards sheep.

6. Goats.—Fig. 17 presents similar data for goats. The goat area was computed by the formula used for sheep. Some of the fetal data for goats are from Barcroft[7] and associates, and others from Gomez and Turner.[8]

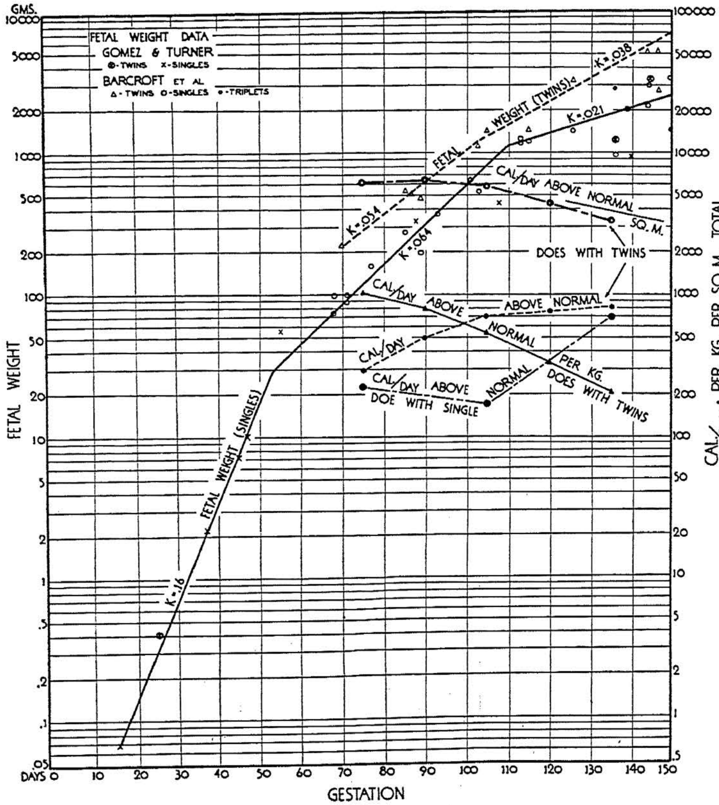


Fig. 17.—Continuation of Fig. 13, but as regards goats.

V. DISCUSSION AND CONCLUSIONS

1. The central empirical quantitative conclusion of this bulletin is that the amount of extra Calories, Q, produced in gestating animals at rest above a similar non-gestating animal under the same conditions of rest is interrelated with the birth weight, M, (in kg.) of the offspring by the equation

$$Q = 4400\ M^{1.2}$$

The numerical values of the constants of this equation are tentative, subject to revision with further accumulation of data. The

[8]Gomez, E. T., and Turner, C. W., The development of the mammary gland of the goat. Mo. Res. Bul. 240, 1936.

importance of this equation does not consist in the precision of its constants, but in its embodiment of an orderly relation between the heat increment of gestation and the birth weight of the offspring.

This equation, derived on the basis of data of different species, states that the production of an offspring (or a litter) weighing 1 kg. at birth is associated with a gestation heat increment of about 4400 Cal., and that the magnitude of this increment varies with approximately the 1.2 power of the birth weight of the offspring.

The equation is rational in the sense that each constant has a definite, understandable, meaning; and empirical in the sense that the theoretical significance of the interrelation has not been elucidated.

2. There is an interesting resemblance between the above equation relating the heat increment of gestation with birth weight, and the Lusk-Rubner "law of constant energy expenditure" during growth (see Graham Lusk, The Science of Nutrition, 1928, p. 567) which reads as follows (Lusk): "To construct one kilogram of normal body substance containing 30 grams of nitrogen and 1722 Calories, 4808 Calories are required except in the case of man, when six times that amount is needed." The 4808 Calories required for constructing 1 Kg. body weight, according to Rubner, is only about 400 Calories more (about 10%) than the 4400 Calories (in our equation $Q = 4400\ M^{1.2}$) associated with the production of an offspring of 1 Kg. birth weight.

It must be remembered that the Lusk-Rubner constant of 4808 includes the energy stored in the fetus, while our 4400 does not include the stored energy.

Moreover, Rubner formulated the "law of constant energy expenditure" with respect to doubling of body weight of the newborn: "The amount of energy (Calories) which is necessary to double the weight of the newborn of all species (except man) is the same per kilograms no matter whether the animal grows quickly or slowly" (Lusk), while our equation refers to the heat increment of gestation, which includes not merely the heat production of the fetus, or of the whole pregnant uterus, but also the increased metabolism of the mother proper as result of the additional burdens and stimulations of the gestating process.

Our equation, also differs from "Rubner's law" in that our equation does not say that 4400 Calories of heat expenditure is associated with 1 Kg. of fetus formation, but that the ratio of the heat increment of gestation to the 1.2 power of weight in kilograms is 4400.

$$\frac{Q}{M^{1.2}(kg)} = 4400$$

The heat expenditure per kg. newborn is 4400 Calories only when the weight of the newborn is 1 Kg.; but if the weight of the newborn is more or less than 1 Kg., then, the heat expenditure per Kg. newborn will not be 4400 Calories, but will vary with the 1.2 power as explained in the text. However, it is not yet certain whether the difference between the value 1.2 of the exponent in the above equation, and the assumed Rubner exponent of 1.0 is significantly outside the limits of variability of the data. Finally, our equation includes humans, while Rubner excepted humans (see quotations from Lusk above).

3. Rubner theorized that his "law of surface area" (Lusk, p. 123) is applicable to prenatal growth. Sandiford and Wheeler, and others[1] reported that their data substantiated Rubner's theory; our analysis, on the contrary, opposes it. The following table (1st 2 columns from Barcroft et al., and the other columns computed by us from Barcroft's data) substantiates Barcroft's and our belief that the "surface law" is not applicable to prenatal growth.

HEAT PRODUCTION IN THE FETAL SHEEP

Fetal age	Weight	Surface	Heat Production, Cal./day		
days	Kg.	Area	Total	Per Kg.	Per sq. meter%
58	0.05	.0146	0.90	18.0	626
98	0.79	.0836	11.40	14.4	136
111	1.40	.120	22.1	15.8	184
112	1.50	.125	29.1	19.4	233
124	1.65	.133	72.4	43.9	544
137	3.60	.218	67.3	18.7	309
138	3.60	.218	59.8	16.6	274
144	4.5	.251	103.5	23.0	412

The heat production per unit area is seen from the above table to be too low by Barcroft's direct method of measuring fetal metabolism; and the preceding charts showing the ratios of excess heat production above non-gestation to fetal area is too high. So we conclude that Rubner's theory of the applicability of the surface law to prenatal growth is not substantiated.