APRIL, 1938 RESEARCH BULLETIN 281

UNIVERSITY OF MISSOURI COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION
F. B. MUMFORD, *Director*

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XLV. Energy-Metabolism Levels During Gestation, Lactation, and Post-Lactation Rest

SAMUEL BRODY, JOHN RIGGS, KENNETH KAUFMAN, AND VIRGIL HERRING

(Publication Authorized April 4, 1938)

COLUMBIA, MISSOURI

CONTENTS

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. In the rat milk production and respiratory quotient fall and rise together with fast and refeeding. Within about 12 hours after the food is taken away from the lactating rat, the R. Q. declines from the initial level of 1 or over, to 0.73, and the milk production (measured by weight increase in litter during 45-minute nursing periods 3 hours apart) declines from the initial level of about 3 grams to zero. On refeeding the mother rat after a 2-days fast, R. Q. and milk production promptly rise to the prefast levels. Hence the tentative inference that in the rat it is not possible to determine the basal (post-absorptive) metabolism during *normal* lactation because *normal* lactation appears to be incompatible with the post-absorptive state. The inference concerning the incompatibility between fast and milk production in the rat suggests the extrapolation to humans, namely that the contemporary opinion that basal metabolism of *normally* lactating women is the same as of non-lactating is mistaken. This extrapolation requires investigation. It is being investigated on cattle and goats. In our experience the heat production of *normally* lactating rats (not in post-absorptive condition) is nearly double that of non-lactating of the same weight.

2. In the rat, the resting energy metabolism (measured by respiratory exchange) during gestation is practically the same as during sex rest of animals of the same size (the ratio $\frac{\text{Cals/day}}{(\text{Wt})^{0.73}}$ remains constant during gestation). In growing cows, the metabolism during gestation tends to increase more rapidly than the 0.73 power of body weight. It is concluded that the body-weight increase during gestation without an apparent food-energy cost is accounted for not by lowering of *resting* metabolism but by: (a) reduction of spontaneous physical activity with a resultant saving of energy which is applied to body-weight increase; (b) saving of heat increment of feeding (S. D. A.) because protein stored for growth does not yield a heat increment (Rubner). (c) Another contributing factor to the small food-cost of weight gain during pregnancy is the rather watery nature of the gestation gains (amniotic fluid about 96% water; placenta and new-born animal up to 90% water) and possibly hydration of mother's body proper during gestation. (d) The maintenance cost of the pregnant uterus may be *relatively* inappreciable because of the thermoneutrality of its environment, and its low tonicity and physical activity. While the *absolute* energy cost of growth may be considerable, it is probably *relatively* (as compared to resting metabolism of mother) insignificant.

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I. INTRODUCTION

1. Some 23 years ago Eckles, at that time Chief of the University of Missouri Dairy Department, concluded on the basis of excellent data,[1] that pregnancy does not involve an increase in feed consumption in dairy cattle. This result is surprising in view of the fact that during gestation mature cows gain about 16% in body weight (see Fig. 1), including the production of a calf, placenta, and related structures which, of course, involve not only constructional but also maintenance expenses.

Eckles' conclusions on cows seem to have been substantiated by Slonaker[2] and Wang[3] on rats (Fig. 2).

The anomalous result of weight gains without food cost suggested the investigation on energy expenditure of *gestating* animals during rest employing the respiratory exchange method. The present paper reports the results on such an investigation on rats, supplemented with a few data on the metabolism of the first gestation in very young dairy cattle.

2. Another surprising result concerns the energy cost of *lactation.* It is generally known that there is an enormous increase in food consumption during lactation; one would consequently expect that there would also be an increase in heat production. But the literature indicates,[4] that there is no increase in heat production ("basal metabolism") during lactation. This conclusion that there is a great increase in food consumption but no increase in heat production during lactation does not seem reasonable. The second object of this paper is to report data on the metabolism of lactating animals (mostly rats, supplemented by a few young cows during rest).

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[1] Eckles, C. H., The nutrients required to develop the bovine fetus. Univ. Mo. Agric. Exp. Sta. Res. Bul. 26, 1916.

[2] Slonaker, J. R., The effect of copulation, pregnancy, pseudopregnancy, and lactation on the voluntary activity and food consumption of the albino rat. Am. J. Physiol. *71,* 362, 1924-5.

[3] Wang, Ging, H., The changes in the amount of daily food-intake of the albino rat during pregnancy and lactation. Am. J. Physiol. *71,* 736, 1925.

[4] See Lusk, G., The science of nutrition, Philadelphia, 1928. See the appendix for a fuller review of the literature.

PAPER 155 IN THE HERMAN FRASCH FOUNDATION SERIES.

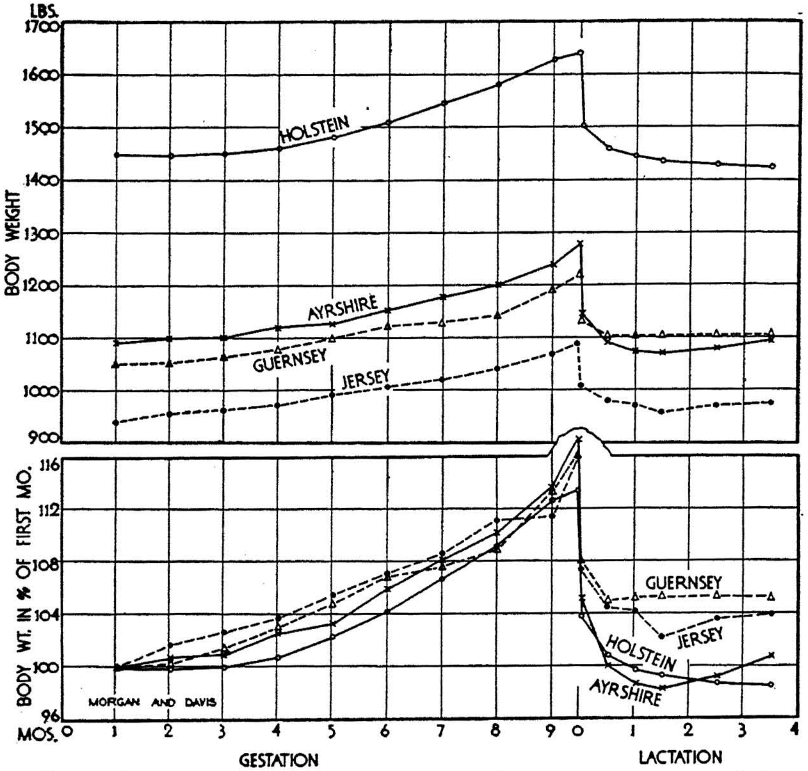

Fig. 1.—The course of changing body weight with advancing gestation and lactation in dairy cattle. Plotted from data by F. R. Morgan and H. P. Davis in Univ. Neb. Agr. Exp. Sta. Res. Bull. 82, 1936.

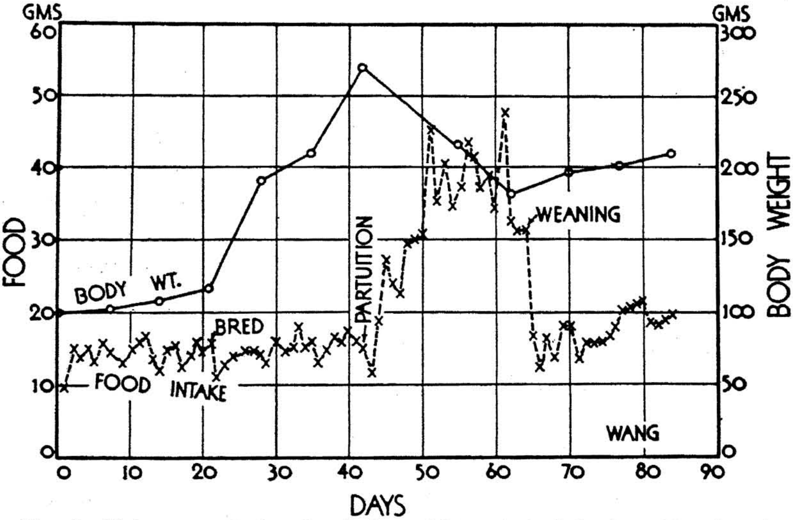

Fig. 2.—The course of changing body weight and food intake with advancing gestation and lactation in the rat. From Ging H. Wang, Am. J. Physiol., 1925, p. 736.

II. THE TIME COURSE OF THE MOTHER'S BODY WEIGHT AND RESPIRATORY EXCHANGE DURING GESTATION AND LACTATION

1. The time course of body weight and metabolism during gestation and lactation on an arithlog scale.

In Fig. 3 (based on Table 1 in the Appendix) body weight and heat production during gestation and lactation are plotted against time on an arithlog grid to emphasize their *relative* changes.

The outstanding feature of Fig. 3 is that it shows that during *gestation* both metabolism and body weight tend to increase. During *lactation*, on the other hand, body weight decreases, while metabolism increases. Assuming that the non-lactating basal metabolism of the rat is 25 calories per day, the lactation metabolic peak is seen from Fig. 3 to be nearly twice the non-lactation metabolic level. The tentative conclusion is that the resting heat production in gestating rats is the same as in non-gestating of the same body weight; but that the heat production in lactating rats is nearly twice that of non-lactating. The remaining charts in this paper substantiate this conclusion.

2. The time course on a logarithmic scale.

It was previously shown[5] that the basal metabolism of mature animals of different species varies with the 0.73 power of body weight; in other words, when metabolism data of mature animals of different species are plotted against body weight on a log-log grid, the resulting slope is of the order of 0.73. While this generalization is based on data for mature animals of *different* species, it seemed interesting to compare our metabolism data during gestation and lactation of the *same* species with this 0.73 power theoretical curve. Such comparison is exhibited in Fig. 4.

The gestation and post-lactation data (circles) are parallel to the theoretical curve; the lactation data (triangles) are not parallel with the theoretical curve. The results in Fig. 4 confirm those in Fig. 3, that if we accept the 0.73 power of body weight (including weight of pregnant uterus) as reference base, heat production during *gestation does not* involve an energy expense beyond that expected. *Lactation does* involve an extra energy expense, which, depending on the milk flow level, may rise to perhaps 100% above the theoretical non-lactating level.

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[5] Cf., Basal metabolism, endogenous nitrogen, creatinine, and neutral sulphur excretions as functions of body weight. Univ. Missouri Agric. Exp. Sta. Res. Bul. 166, p. 93, 1932; Id., Res. Bul. 220, 1934.

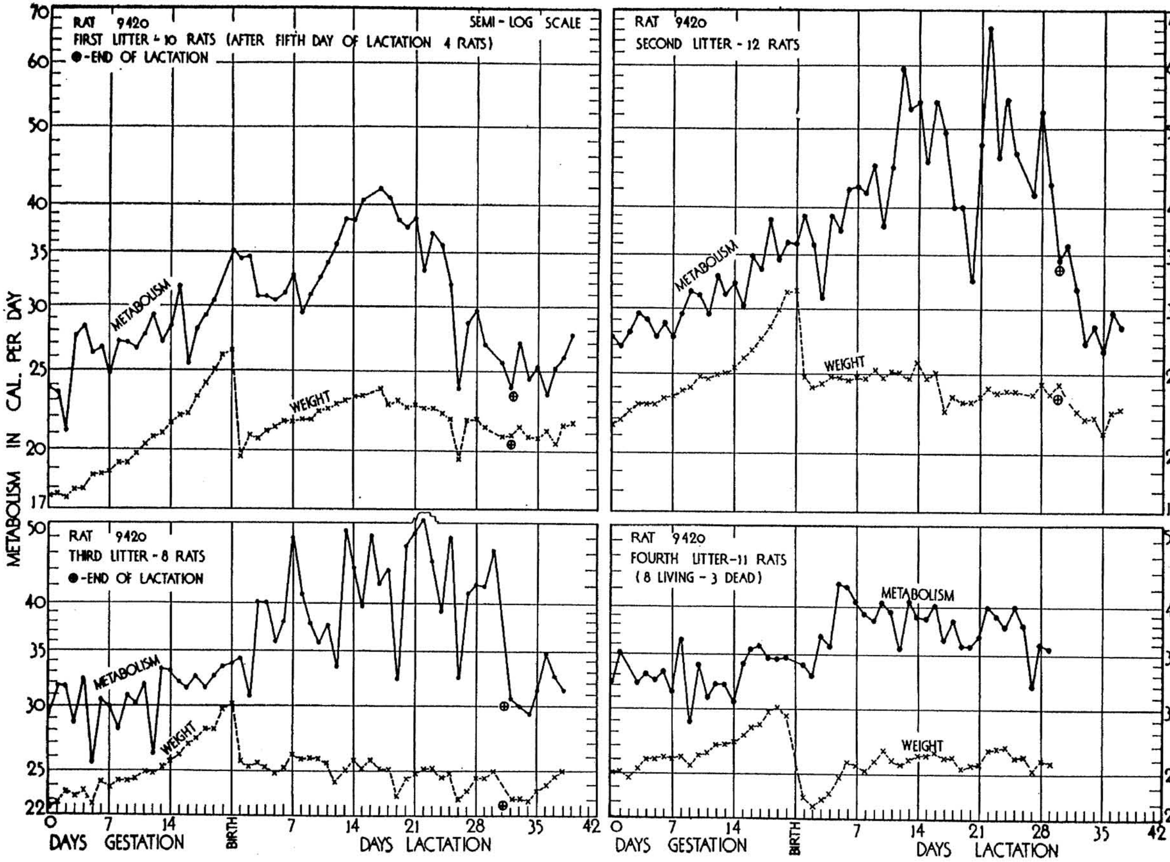

Fig. 3.—The course of body weight and heat production during gestation and lactation in the rat plotted on an arithlog grid (slope represents not absolute increase as on arithmetic paper, but relative change, or percentage when multiplied by 100).

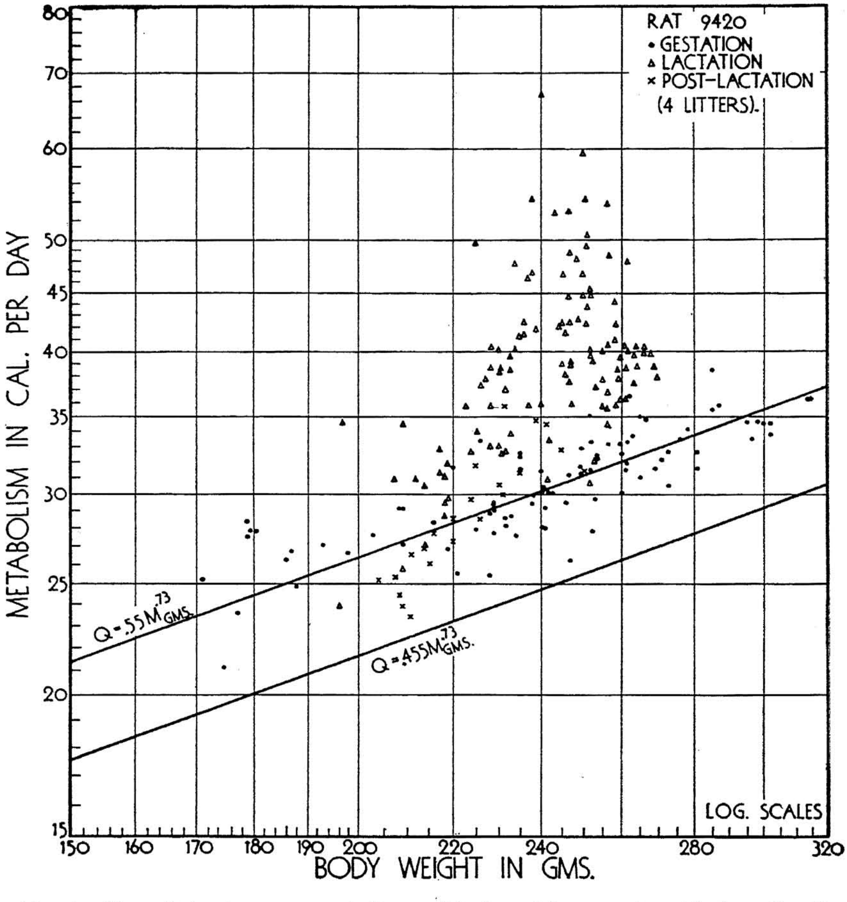

Fig. 4.—The relation between metabolism and body weight on a logarithmic grid. The curve of the equation $Q = 0.455\ M^{0.73}$ represents the relation between basal metabolism, Q, and body weight, M, of mature animals of different species as reported in Missouri Ag. Exp. Station Res. Bul. 166 (1932), and 220 (1934).—Circles represent gestation data, crosses post-lactation rest data; triangles represent lactation data. Note the higher level of the lactation data as compared to the sex-rest and gestation data.

3. The time course of the ratio heat production to the 0.73 power of body weight.

Assuming that *physiologic* weight[6] is directly proportional to the 0.73 power of gravitational or *physical* weight, then the ratio $\frac{\text{Calories}}{(\text{Wt})^{0.73}}$ should indicate the relative influence of gestation and lactation on metabolism. The time course of gestation and lactation for such a ratio is shown in Fig. 5. The curves in Fig. 5 show clearly that for

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[6] Cf., Brody, S., Relativity of physiologic time and physiologic weight, GROWTH, *1*, 60, 1937.

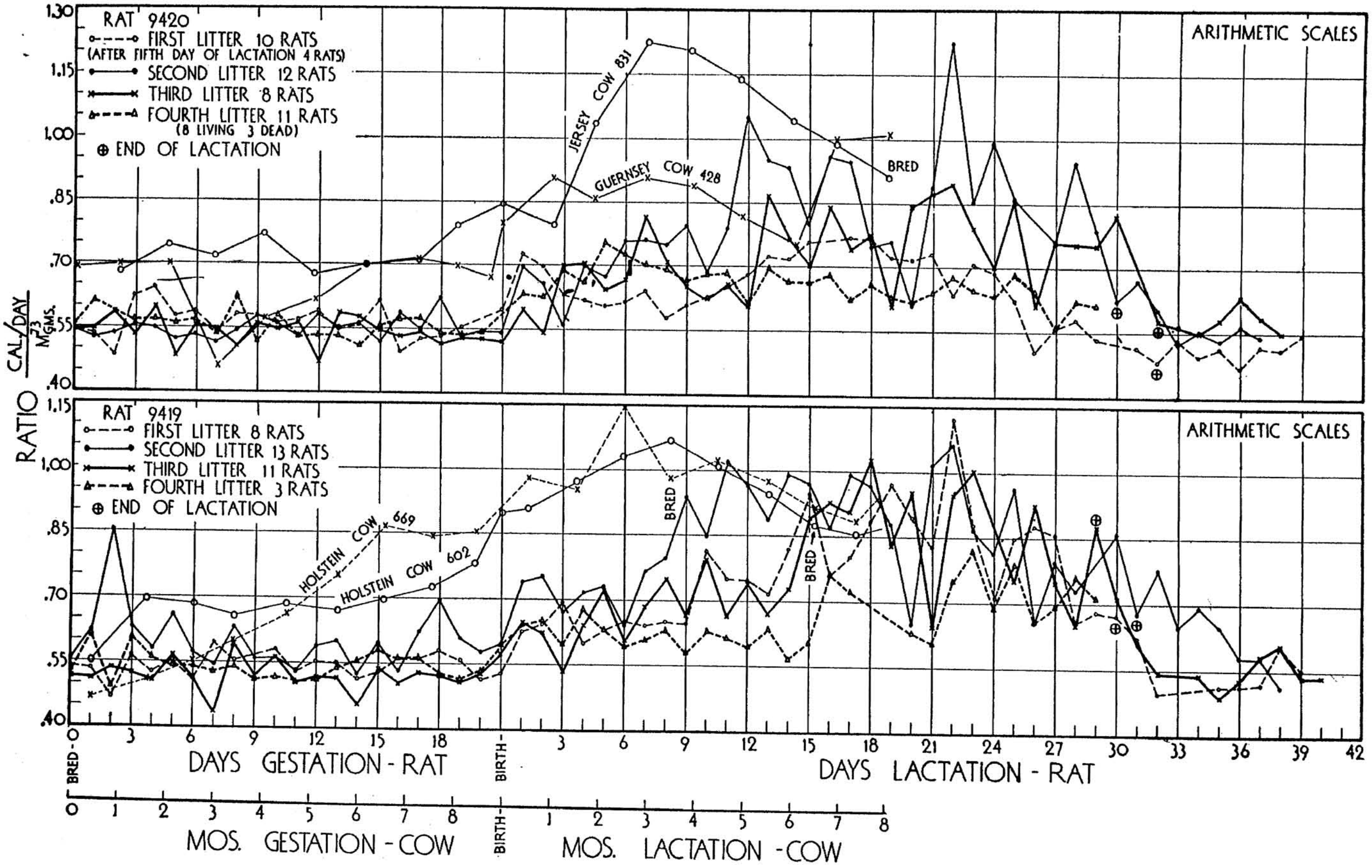

Fig. 5.—The time course of the ratio $\frac{\text{Cal./day}}{(\text{Wt})^{0.73}}$ with the advance of gestation and lactation in rat and cow. In the rat, this ratio is unchanged during gestation; in the cow it is increased during the last month or two; in both species it is greatly increased during lactation.

rats the ratio $\frac{\text{Cal./day}}{(\text{Wt})^{0.73}}$ is roughly constant, namely about 0.55 during the period of *gestation*, but nearly double this value during *lactation*. For cows, the ratio $\frac{\text{Cal./day}}{(\text{Wt})^{0.73}}$ is higher, and tends to increase somewhat with the period of gestation.

4. **The time course in terms of the percentage of initial values on an arithmetic scale.**

The most understandable method of representing the relative influence of gestation and of lactation on body weight on one hand and metabolism on the other is to represent each as percentage change of the same standard value (such as the values during the first day of gestation). Figs. 6a and 6b represent such percentage changes on an arithmetic grid taking the first day of gestation as standard for: (a) body weight; (b) metabolism; and (c) metabolism per $(\text{Weight})^{0.73}$, assuming that $(\text{Weight})^{0.73}$ is the *physiologic weight* as contrasted to

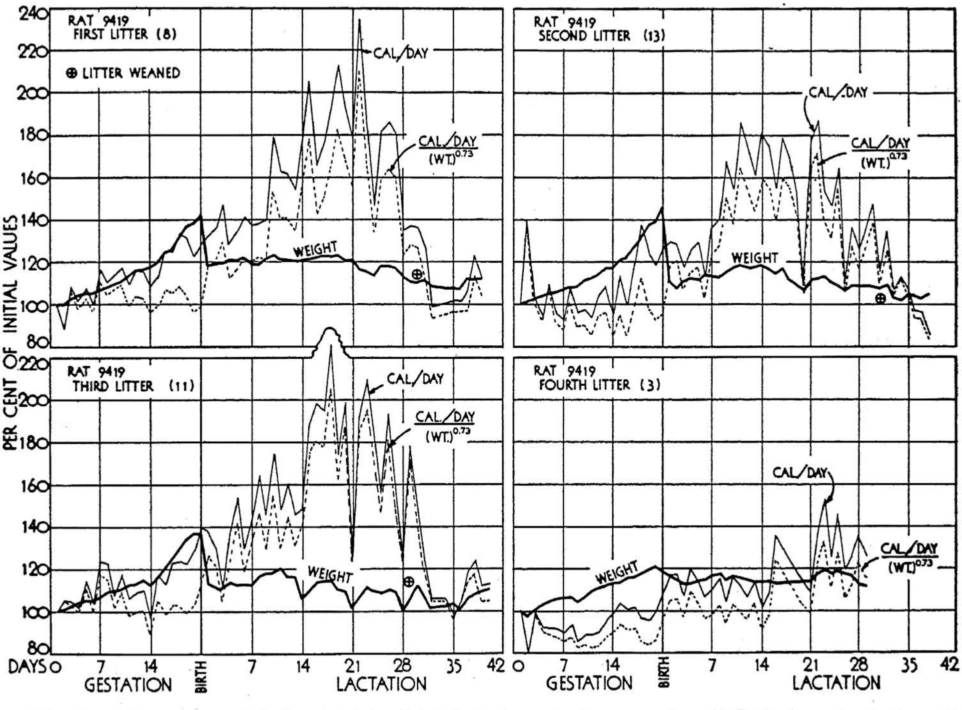

Fig. 6a.—The course of body weight, of total heat production per day (Cal./day), and of the ratio $\frac{\text{Cal./day}}{(\text{Wt})^{0.73}}$ plotted in terms of percentage of the values on the day of breeding.

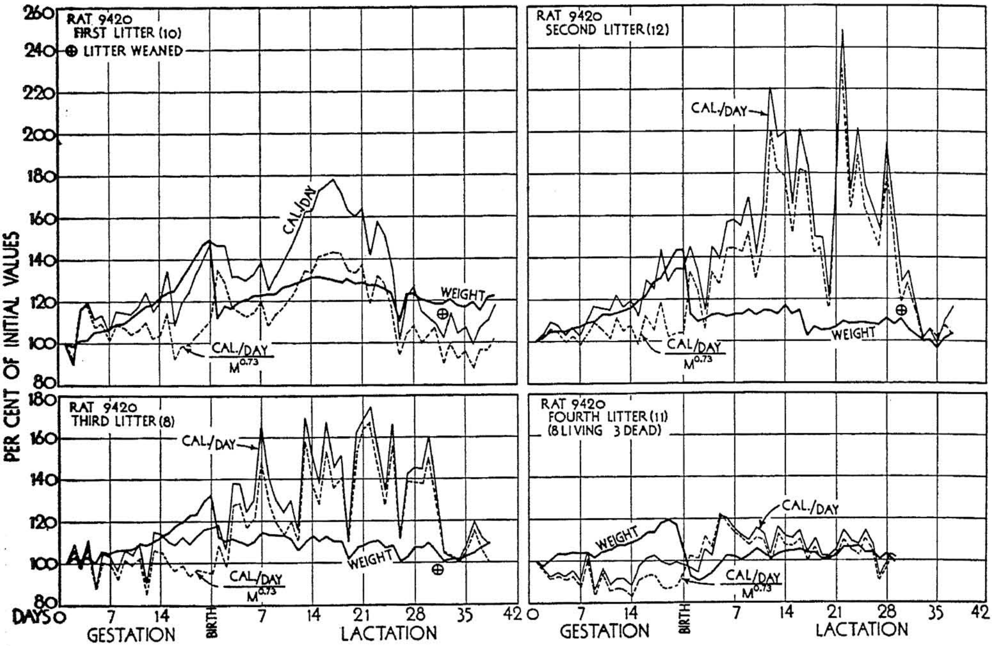

Fig. 6b.—Similar data as in Fig. 6a but for another rat.

simple weight. Fig. 6 which is self-explanatory, confirms the conclusions of Figs. 3 to 5.

This section may be summarized by the statement that in rats the metabolism of gestation is not increased beyond the normal proportion for the weight increase; that is, the ratio metabolism to $(\text{Weight})^{0.73}$ is within the errors of the work unaffected by gestation. The metabolism of lactation, on the other hand, is enormously increased beyond the normal proportion for the weight increase; that is, the ratio metabolism to $(\text{Weight})^{0.73}$ is greatly increased by lactation.

III. FOOD CONSUMPTION AND THE SPECIFIC DYNAMIC ACTION IN THE MOTHER DURING GESTATION, LACTATION, AND POST-LACTATION REST.

According to the literature (see appendix) lactation in humans does not increase the basal energy metabolism. Yet the preceding section made it clear that lactation in the rat and cow increases heat production to a high level. Does this increase in metabolism during lactation represent the energy expense for "making" the milk? Does it rep-

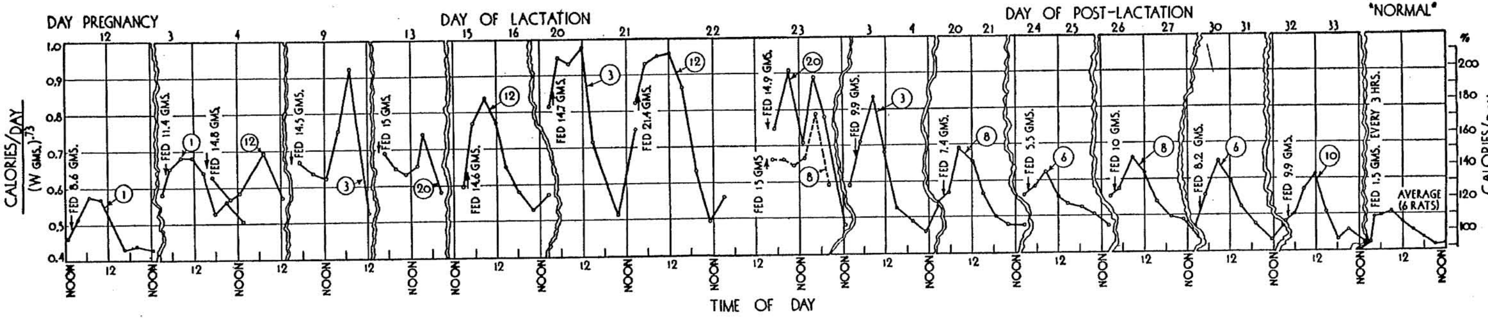

Fig. 7.—The course of food consumption after 12 hours fast, and of heat production per $(Wt)^{0.73}$, with the advance of the stage of gestation and lactation. Since this research involved fasting the 12 hours before and about 12 hours following the meal, it was not desirable to use the same animals for successive measurements during gestation and lactation. Different animals were therefore used, and the numerals in the circles refer to the laboratory numbers of the rats. The upper scale indicates day of gestation, lactation, and sex rest (rats weaned at age 21 days). The lower scale indicates time of day, since it was previously shown (Mo. Res. Bul. 274) that there is a very considerable diurnal metabolic rhythm. The left scale represents the ratio $\frac{\text{Cal./day}}{(\text{Wt})^{0.73}}$, while the right scale represents the same ratio in terms of the percentage of the assumed basal metabolic level of rats in sex rest (when this ratio = .45).

resent the energy expense of feed utilization (specific dynamic action)?

The curves in Fig. 7 were prepared in the attempt to throw light on this question. Fig. 7 pictures the influence of feeding and fasting in the rat on heat production during: (a) sex rest, (b) gestation, (c) lactation, (d) and post lactation.

The extreme right curve in Fig. 7 represents the heat production during sex rest in rats when fed $\frac{1}{8}$ of the daily maintenance ration at 3-hour intervals day and night. (The maintenance ration was 12 gm. a day fed 1.5 grams every 3 hours.) When thus fed, the animals exhibited a slight metabolic rhythm, diurnal in origin as explained in the preceding report.[7] (The left axis of ordinates in Fig. 7 represents metabolism in terms of the ratio Cal. per day/(Weight)$^{0.73}$. The right axis represents this ratio in terms of percentage of the assumed basal value, that is of 0.455 (Weight)$^{0.73}$).

Rat 10, second from the right, was in post-lactation rest. She consumed 9.9 grams feed at the end of a 12-hour fast. Her metabolic rise is above those fed 1.5 grams at 3-hour intervals. (The diurnal rise, of the former was about 10% above the assumed basal; of the latter about 33% above basal.)

We may now observe rat 1 on the extreme left, in the 12th day of *gestation*. She consumed no more after a 12-hour fast than did sexually resting rat 10 on the right of the chart; which leads to the conclusion that *gestation does not call for additional food-energy.*

During *lactation* on the other hand, Fig. 5 shows that the food consumption in a single (45-minute) meal after a 12-hour fast was greatly increased. (The feed consumption values recorded in Fig. 7 were obtained in all cases 12 hours after the preceding meal.) The rise in metabolism after the meal was likewise greatly increased during lactation. In some cases the lactation metabolism is double the resting value (see in Fig. 7 peak metabolism values of rats 3, 12, 20 during the 21-23d day of lactation).

Fig. 7 makes it clear that the *peak metabolism* during lactation is very much higher than the peak metabolism during sex rest or during gestation. The *lowest* (*basal?*) metabolism value during lactation is also higher than during post lactation or gestation; however, the difference is not great, perhaps not significant. If we assume that the difference between the basal values of lactating and non-lactating metabolism in Fig. 7 is not significant, then our results on rats confirm the published results on humans that lactation does not increase *basal* energy metabolism. However, is it not possible that withholding

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[7] **Herring, V. V., and Brody, S., Diurnal metabolic and activity rhythms. Univ. Missouri Agric. Exp. Sta. Res. Bul. 274, 1938.**

food from the lactating animal until basal metabolism is reached, also seriously depresses or even temporarily stops lactation, and that the normal basal metabolism of the animal is the result of this depressed lactation? The following section presents results throwing light on the question as to whether or not the fast involved in reaching post-absorptive condition also depresses the lactation process.

IV. THE INFLUENCE OF POST-ABSORPTIVE CONDITION AND FAST ON MILK PRODUCTION

As previously noted, the literature indicates that basal (post-absorptive) energy metabolism is practically the same during lactation as during sex rest, and we suggested the idea that the basal (fasting) metabolism is low not because lactation does not involve increased metabolism but because lactation is profoundly depressed by the fast involved in reaching post-absorptive condition. *Does lactation decline and finally cease on approach to post-absorptive condition?* Let us investigate this problem first on rats, then on cows and goats, and later on humans. Let us begin by withholding food from a lactating rat, and observe the consequences on her lactation performance.

1. The influence of prolonged fast (6 days) on lactation and respiratory metabolism of rat and litter.

Fig. 8a presents on an arithlog grid, and Fig. 8b on an arithmetic grid, the influence of fast on: (a) body weight (upper curves); (b) metabolism per day (middle curves); and (c) respiratory quotient of rat 1032 and her litter, and (d) the "food intake" of litter (lower curve).

Before proceeding with the discussion the following details need be noted. The numerical data for Figs. 8a and 8b are presented in Table 2 in the Appendix. The metabolism measurements of mother, and of litter, were made in parallel during the same periods, but of course in different metabolism chambers. From Table 2 it is seen that the metabolism record was usually made over 120-minute periods, although occasionally it was prolonged to 240 or even 300 minutes (that is, for 240, or 300 minutes for the mother, and 240, or 300 minutes for the litter). Immediately following the removal of the rats from the chamber, the litter was weighed and allowed to suckle the mother for 45 minutes. The litter was weighed again after the 45-minute suckling period. The weight gained by litter during suckling is designated on the chart as litter "food intake." In other words, milk production in the rat was gauged by the gain in body weight of the suckling litter during 45-minute periods at approximately 3-hour intervals. The actual milk intake was of course

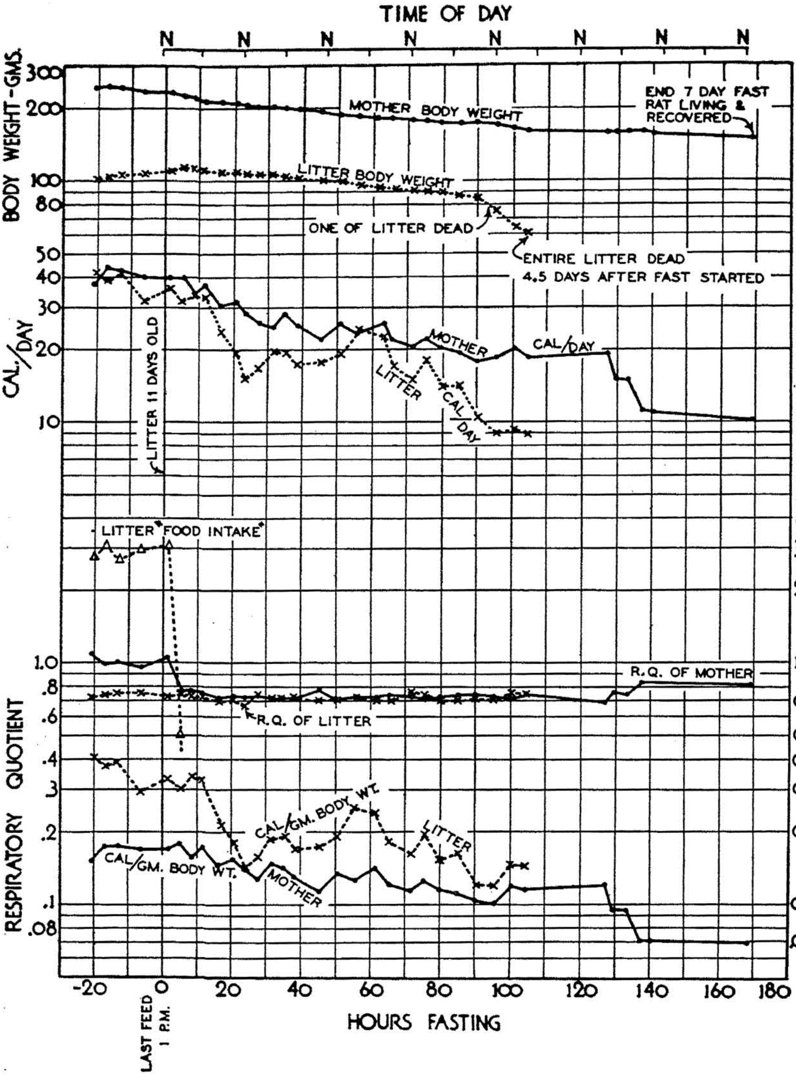

Fig. 8a.—The course of: heat production (Cal./day and Cal./kg./day), of respiratory quotient, and litter "food intake," with time after feeding of the mother. Note the parallelism between the R. Q. of the mother and the "food intake" of the litter. One thesis of the present paper is that the low *basal* (that is fasting) heat production is due not merely to the disappearance of the specific dynamic action of the food, but also to the decline in milk production. In brief, basal (fasting) metabolism does not represent normal lactation metabolism because lactation is depressed on reaching the condition of fast required for basal-metabolism measurements.

higher, because during suckling there was a weight loss due to insensible perspiration and to losses of excreta. Immediately after nursing and weighing, another metabolism record was begun and so on.

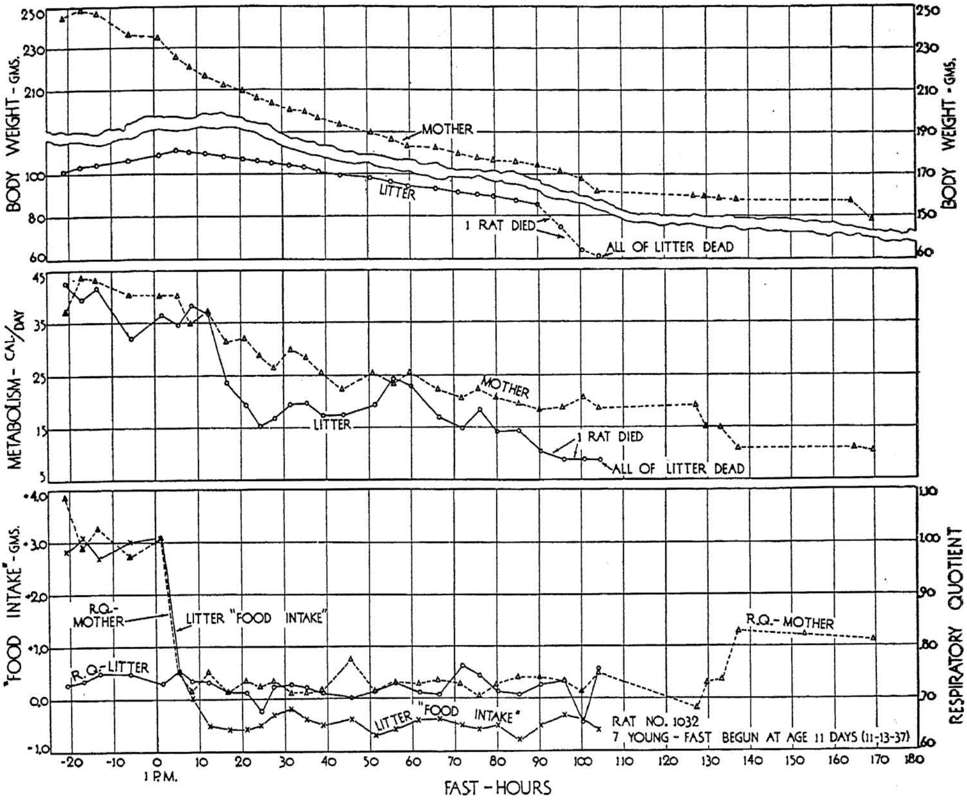

Fig. 8b.—The data plotted in Fig. 6 on arithlog grid are here represented on an arithmetic grid. Note again that the gain in weight of the litter during 45-minutes of suckling declined from 3 gm. to zero within 8 hours after the food was taken away from the mother.

We may now consider Figs. 8a and 8b.

When the mother was on full diet, the litter "food intake" was about 3 grams during a 45-minute suckling interval, with intervals between suckling of about 3 hours. During fast (see Fig. 8 showing removal of last food at 1 p. m.), this program of 3 hour away and $\frac{3}{4}$ hour with mother continued as when the mother had access to food. When the litter was placed for the 3d nursing with the mother at 9:10 p. m., that is 8 hours after the food was removed from the mother, the litter failed to gain in weight during the 45-minute nursing period. (See the 3d point, that is 3d suckling period, on the litter "food intake" curve in Fig. 8b.) Following the 3d suckling, 8 hours after the food was removed from the mother, the litter *lost* about $\frac{1}{2}$ gram at each suckling. The litter was eleven days old when the mother's fast began.

Since the mother rat requires *at least* 8 hours to reach post-absorptive condition, and since the litter failed to secure appreciable milk 8-hours after feeding, it is concluded that *lactation in this species at least tends to be greatly depressed on approaching post-absorptive condition.* This fact suggests that the low *basal* (post-absorptive) metabolism in lactating women as recorded in the literature, may not be an indication that lactation does not involve an energy expense, as postulated by Lusk and others; but that *lactation was depressed to a very low level during post-absorptive condition,* and consequently the metabolism was likewise depressed.

Before leaving Figs. 8a and 8b attention may be called to the following additional features which do not bear directly on the problem under consideration.

While the litter survived only 4 days after the food was removed from the mother, the mother survived seven days, and completely recovered on refeeding. This indicates that milk is not produced at the expense of the mother's stable tissues, otherwise milk secretion would continue and the litter would survive nearly as long as the mother.

Another interesting aspect is that when the 7-infant litter was 10 days old, its heat production was equal to that of the mother (about 45 Cal. per day) and in the same time it gained about 12 grams a day in body weight, which is equivalent to an energy storage of about 18 Calories. The mother rat must have, therefore, produced at least 63 Calories of milk energy per day (45 metabolism, 18 Cal. body storage). This is equivalent to about 1/10 quart or 100 cc of average cows milk; which weight of cows milk is about 40% of the mother-rat's body weight.

It is, moreover, interesting to note that the ratio of daily milk energy produced (60-70 Cal.), to *basal metabolism* (25 Cal.) is from 2 to 3. This ratio of milk calories to basal metabolism calories is within the limits found in dairy cows. In "ordinary" cows, the ratio $\frac{\text{Milk calories}}{\text{Basal met. cal.}}$ is about 1.7; in "extraordinary", champion cows, this ratio may reach 3.8. But the ratio of milk calories to *body weight* (in Kg.) is $\frac{60}{0.25} = 240$ in rats, while in cows it is about 2 $\frac{1100}{510}$ in "ordinary" cows, and 40 and 60 respectively in the present Holstein and Jersey Champions. In other words, the ratio of milk energy to *basal metabolism* energy is independent of size of animal, but the ratio of milk energy to *body weight* rapidly decreases with increasing weight. In brief, *milk secretion tends to be proportional not to body weight, but to basal metabolism.*

2. **The influence of short fasts (32-42 hours) and subsequent refeeding on lactation and respiratory exchange of rat and litter.**

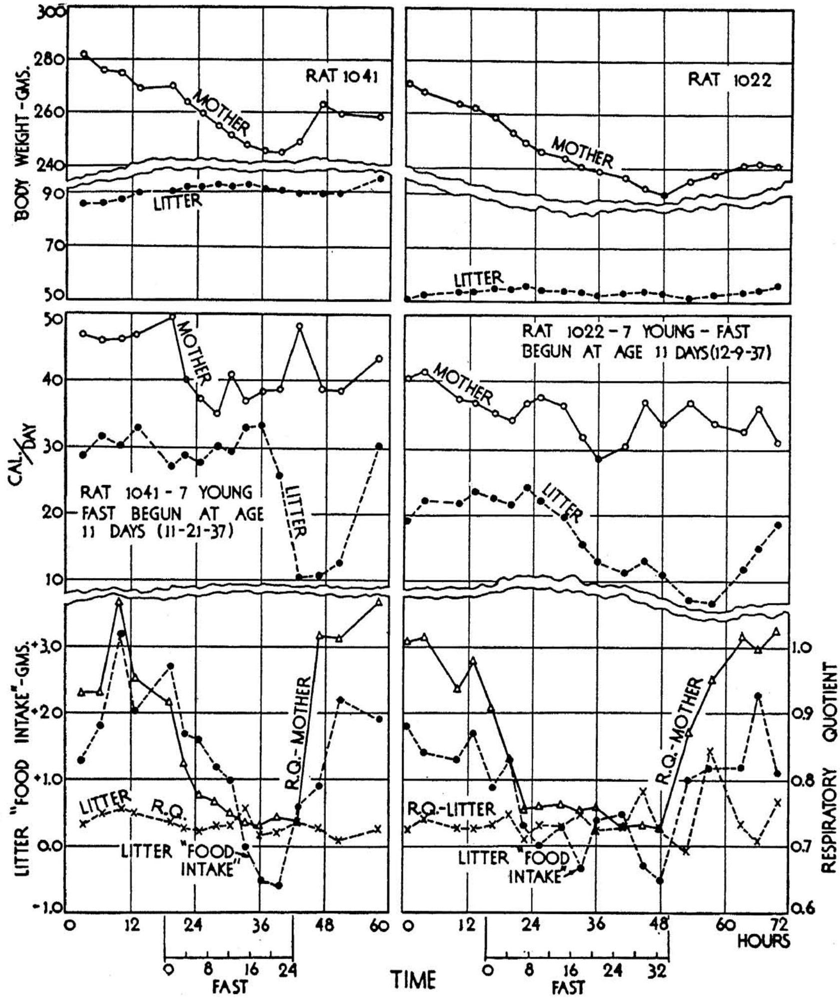

Fig. 9a.—The influence of fasting and refeeding of mother on her milk production (measured by litter-weight gain during suckling), metabolism, body weight, and R. Q. Note the prompt decline in "litter food intake" and metabolism on fasting and rise on refeeding.

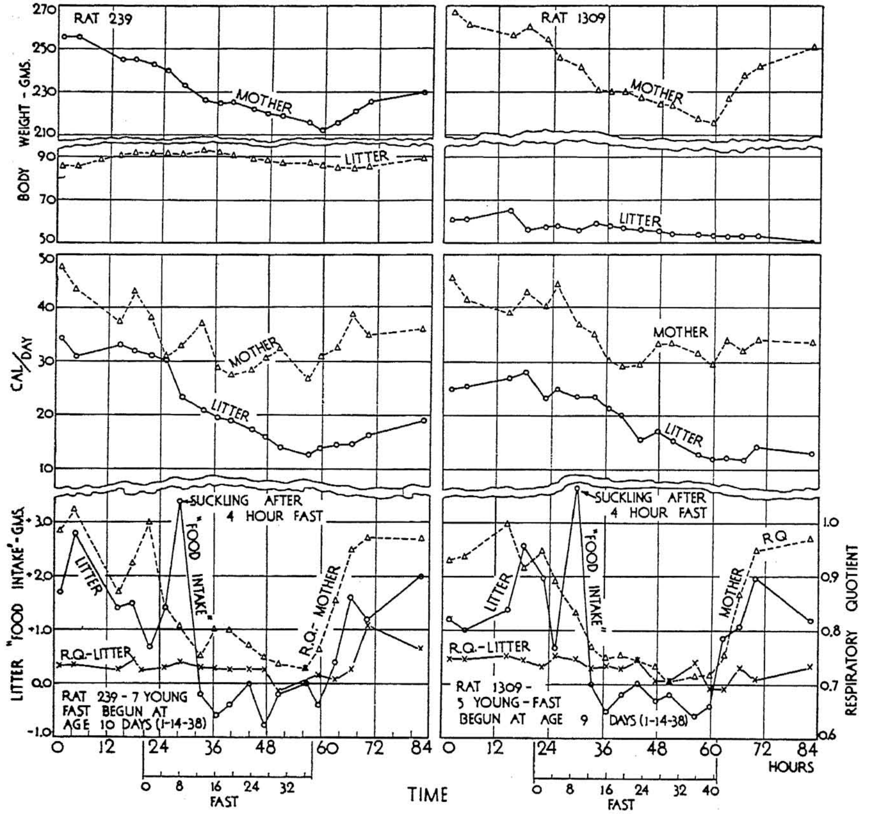

Fig. 9b.—Same as 7b for somewhat longer fasts (38 to 40 hours) and refeedings, which substantiates the data in Fig. 7a.

Figs. 9a and 9b representing the rise and decline of milk production with fast and refeeding, based on Tables 3a and 3b, in the appendix confirm the conclusion drawn from Fig. 8 that lactation in the rat declines rapidly on approach to fasting state. Litter 1041 (left curve Fig. 9a) failed to gain in weight during suckling 16 hours after the food was taken from the mother. Litter 1022 (right side Fig. 9a) failed to gain 9 hours after the food was taken away from the mother, but it gained somewhat at 13 hours and also at 20 and 26 hours after food taken from mother. However, the gains during fast of mother were very slight in comparison to the gains during customary feeding. Litter 1041 (left Fig. 9b) failed to gain 12½ hours after the food was taken from the mother, and rapidly lost after that. Litter 1039 (right Fig. 9b) failed to gain 9 hours after the food was taken from the mother, but erratic gains were made at later hours.

While there appear to be many individual variations (dependant on size and vigor of litter, condition of mother etc.), it seems from Figs. 9a and 9b that, in general, *lactation in the rat is profoundly depressed on approach to the fasting state,* and that, consequently, a *low basal (post-absorptive) energy metabolism is not an indication that lactation does not involve an energy expense.* Obviously, more data are needed on humans as well as on other species in order to solve this problem, and such data are being collected in this laboratory on cows and on goats.

A most interesting aspect of Figs. 9a and 9b is that after lactation apparently stops due to fast in mother, it is promptly resumed on refeeding the mother. This is shown in Figs. 9a and 9b by the change in slope from declining to rising of the time curves on food intake, body weight, and metabolism of the litter. Again note the striking parallelism between the R. Q. of mother and food intake of litter. The change in slope of these time curves demonstrates that the lactation apparatus apparently was not impaired by the fast, and that food is the only limiting factor (water was available).

3. **The respiratory quotient of litter and mother.**

It is not possible to gauge the fasting condition of the litter by its respiratory quotient because even during abundant feeding the litter R. Q. does not rise above 0.75. The mothers R. Q. on the contrary, declines from over 1.00.

The reason for the low litter R. Q. may be found in the peculiar composition of rat milk. According to Cox and Mueller[8] rat milk contains 14.8% fat, 2.8% carbohydrate, and 11.8% protein. The non-protein R. Q. of the milk is therefore 0.73. (The non-protein fat percentage $= \frac{14.8 \times 9}{14.8 \times 9 + 2.8 \times 4} = 92\%$, which corresponds to an R. Q. of 0.73.) The litter R. Q. is raised to 0.74 or 0.75 because of some protein oxidation. The non-protein R. Q. of the infant rat is near 0.73 because the non-protein R. Q. equivalent of its mother's milk is near 0.73; so that change in R. Q. in the infant rat is not an index of its nutritive condition. For this reason we preferred changes in the body weight in food intake, and in metabolism of the litter rather than R. Q. as nutritive indices. These indices are carefully plotted in Figs. 9a and 9b, and the numerical details are given in Tables 3a and 3b.

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[8] Cox, W. M., Jr., and Mueller, A. J., The composition of milk from stock rats and an apparatus for milking small laboratory animals. J. Nutrition, *13*, 249, 1937. See also Mayer, D. T., Rat's milk and stomach contents of suckling rats. J. Nut. *10*, 343, 1935.

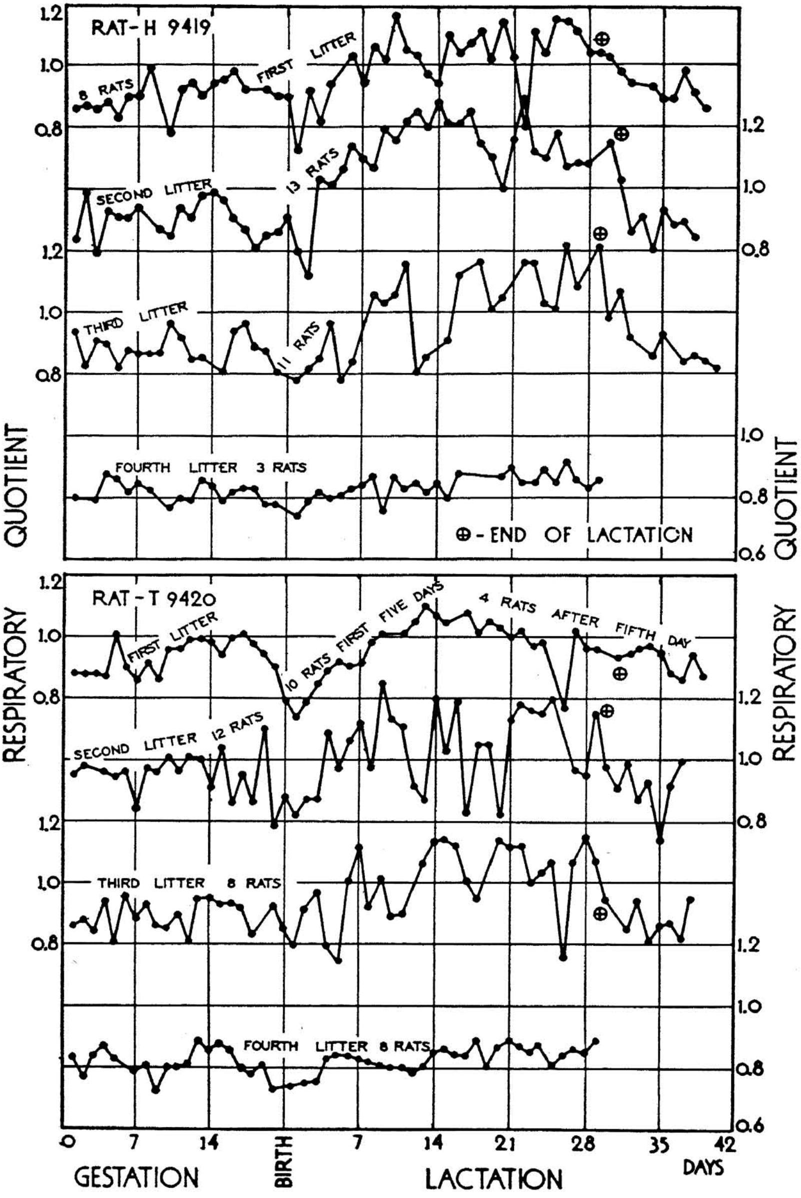

Fig. 10.—The course of the respiratory quotient of the rat with the advance of gestation and lactation. Note the exceptionally high R. Q. during heavy lactation.

The mother's R. Q. during fast follows the expected course as indicated by Figs. 8 and 9. Fig. 10 shows the course of R. Q. of normally-fed rats during gestation and lactation. Fig. 10 shows a tendency for the R. Q. to decline during the parturition period and first day of lactation, and rise above unity, in some cases to 1.2 during the height of lactation—reflecting synthesis of fat from dietary carbohydrate for the fat-rich rat milk.

4. **Summary.**

Milk production in the rat declines on approach to a condition of fast, and consequently a low *basal* (post-absorptive) energy metabolism is not an indication that the normal lactation level does not elevate metabolism, or that there is no energy expense in normal lactation. It was noted incidentally that 48-hours fast does not impair lactation as indicated by the fact that on refeeding, lactation was resumed at the pre-fast rate. It is also noted incidentally that the litter R. Q. during abundant feeding does not exceed 0.75 because of the high fat content of rat milk.

V. DISCUSSION AND CONCLUSIONS

1. One conclusion of this paper is that *normal* lactation rate is not compatible with the post-absorptive condition required for basal-metabolism measurements; and that for this reason basal metabolism during lactation does not include the energy expense of normal milk production.

Is the above conclusion, based on observations on rats, applicable to humans? If so, then the current belief (see review of literature in appendix) that the basal metabolism of lactating women is the same as of non-lactating is mistaken.

The conclusion that lactation nearly stops on reaching post-absorptive condition does not seem to be entirely applicable to dairy cows. Cows continue milk production at declining rates but increasing fat percentages for perhaps a week of fast. But this is only another way of saying that a week of fast in the cow is with respect to its effects on milk production biologically equivalent to a day of fast in the rat.

The above conclusion suggests the following questions to students of lactation and metabolism in the human mother: What is the effect of withholding food for different intervals of time on milk production and metabolism in humans? Does milk production in the human continue at the normal rate in post-absorptive condition?

The above conclusion suggests the following questions to students of comparative metabolism and lactation: What are the biologically

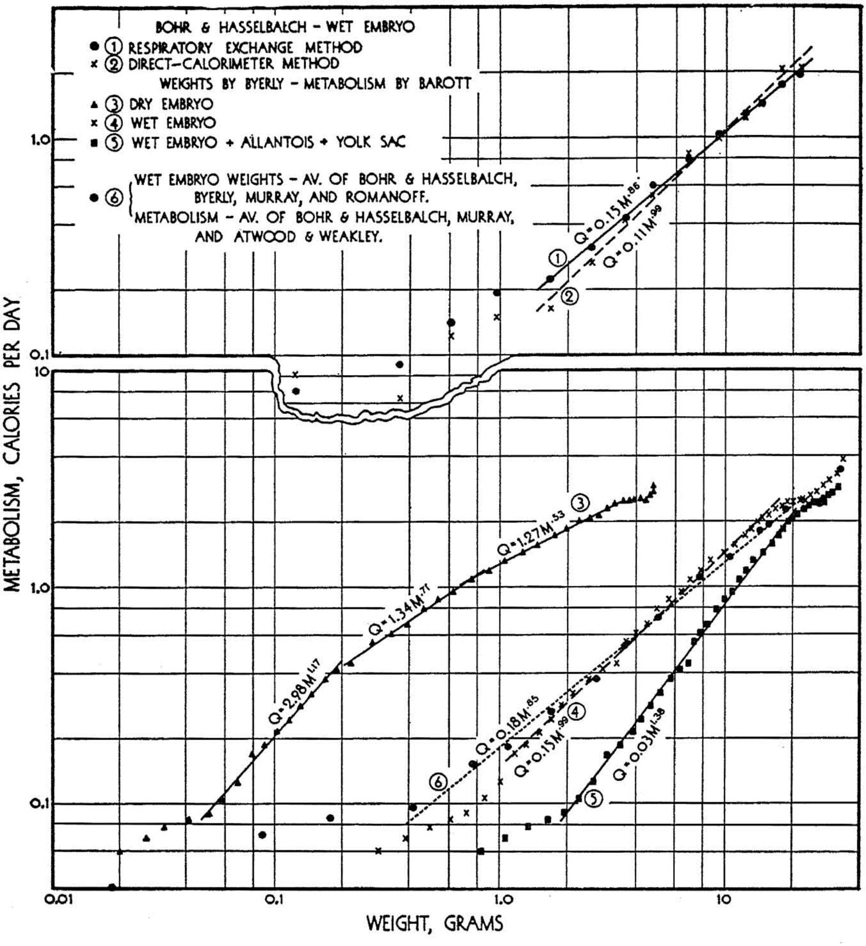

Fig. 11.—The course of heat production in the chick embryo plotted from sources indicated on the chart. This chart shows that heat production does not increase with the surface area (i. e., with the ⅔ power of body weight) of the embryo.

equivalent time intervals of fast, with respect to their influence on milk production, in different mammals corresponding to a day in the lactating rat? Does a given respiratory-quotient level (i.e., ratio of carbohydrate to fat oxidized) have the same significance with regards to milk-secretory activities in different species? If so, is the blood-sugar level ordinarily the first limiting factor in milk production during fast? Or is the R. Q. only symptomatic of a decline of all milk precursors in blood?

2. The second contribution of this paper, that the resting metabolism in the gestating rat is the same as in the non-gestating of the same body weight, suggests several implications: *a.* Since the body weight increases during gestation, the metabolism likewise increases (with the 0.73 power of body weight). Therefore, while at rest a gestating animal expends more energy than a non-gestating. *b.* Since, however, the gestating animal does not apparently consume more food energy than the non-gestating, in spite of the fact that the gestating spends more energy (per animal) and in addition makes new growth, the conclusion follows that in gestating animals energy is saved in other ways such as: reduction of physical activity (Slonaker, Wang, Richter), reduction of heat increment of feeding or S.D.A. (Rubner), and reduction of muscular tonicity. *c.* The data presented in this paper do not shed light on the problems of maintenance of the new growth, or on the energy cost of the growth. The cost of growth and maintenance of fetus is too complex: the weight increase during gestation is mostly (perhaps 90%) water; the fetus lives under conditions of perfect thermoneutrality, complete physical inactivity; the energy expense of growth is small in comparison to the normal maintenance expense of the mother.

In the cow and human, metabolism increases more rapidly than is expected from the $\frac{2}{3}$ or 0.73 power relation. The situation is too complex for attributing this metabolic increase to the increasing surface area of the fetus especially since little is known concerning the *physiologically effective* surface of the fetus and applicability of the "surface law" to intrauterine life. We have plotted in Fig. 11 heat production as function of body weight in the chick embryo on a log-log grid. If the "surface law" were applicable, then the numerical value of the exponent would be 0.67, which evidently it is not. It is more rational to attribute the increased metabolism above the expected level to the known increased endocrine (especially pituitary and thyroid) activities during gestation.

VI. APPENDIX.

A. Review of Literature

With one or two exceptions, which will be specifically noted in the text, the published data are concerned with pregnancy and lactation in humans. Among the best known general reviews are those by Lusk,[9] Needham,[10] DuBois,[11] Harding,[12] and Feldman.[13]

1. **Gestation metabolism.**—Harding did not doubt that there is an increase in heat production during gestation and he posed three questions concerning this increase. (1) Is the increased basal metabolism during gestation the result of simple increase in body weight as it would be of a heavier non-gestating individual? (2) Is it the resultant as of a non-gestating individual plus the metabolism of another individual, namely the fetus? (3) Is there an increased heat production level because "there is something inherent in pregnancy itself which may affect the energy exchange in some incalculable manner?" The following notes indicate that there are defenders of each of the above possibilities.

Carpenter and Murlin[14] concluded that the maternal organism and fetus function as two separate units in their energy consumption; because the metabolism of a pregnant mother shortly before parturition was nearly the same as of mother *and* child after childbirth. Sandiford and Wheeler[15] came to similar conclusion on the basis of separately computed metabolism of fetus and of mother (the metabolism was expressed in relation to the sum of the surface areas of mother and fetus), which agreed with the observed metabolism of the gestating mother.

Rowe and Boyd[16] criticized Sandiford and Wheeler: "They (Sandiford and Wheeler) reached the conclusion that the foetal metabolism, as correlated with the surface changes engendered by foetal growth, was adequate to account for the difference. The study of a single case makes no allowance for the variations recognized to occur normally in this magnitude—the conventional allowance of ± 10% in defining the zone of normal performance. . . . . We are in-

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[9] Lusk, G., The Science of Nutrition, Philadelphia, 1928, p. 529.

[10] Needham, J., Chemical Embryology, Cambridge, 1931.

[11] DuBois, E. F., Basal metabolism in health and disease. Philadelphia, 1936.

[12] Harding, V. J., Metabolism in Pregnancy, Physiol. Reviews, 5, 279, 1925.

[13] Feldman, W. M., The principles of ante-natal and post-natal child physiology, London, 1920.

[14] Carpenter, T. M., and Murlin, J. R., The energy metabolism of mother and child just before and just after birth. Arch. Int. Med. *7*, 184, 1911.

[15] Sandiford, I., and Wheeler, T., The basal metabolism before, during, and after pregnancy. J. Biol. Chem. *62*, 329, 1924; Sandiford, I., Wheeler, T., and Boothby, W. M., Metabolism studies during pregnancy and menstruation. Am. J. Physiol. *96*, 191, 1931.

[16] Rowe, A. W., and Boyd, W. C., The metabolism in pregnancy, J. Nutrition, *5*, 551, 1932. See also: Rowe, McManus and Riley, Id., *7*, 591, 1934; Rowe, A. W., Alcott, M. D. and Mortimer, E., Changes in the basal metabolic rate during pregnancy. Am. J. Phys. *71*, 667, 1925.

clined to question the convention adopted in the two papers under discussion, of subtracting the foetal from the maternal weight before computing the latter area. Certainly the increase in the pelvic and abdominal contents produces a definite increment in the surface area of the mother. A more rigorous analysis of the existing data can be secured through determining the excess heat production due to the foetus by deducting the maternal from the total caloric production and then comparing these values with the foetal area." Rowe and Boyd then proceeded to attribute the increased heat production to "specific foetal influence." "The excess heat production is apparently the result of a complicated and unknown mechanism, engendered by the state of pregnancy but involving other factors than those of foetal tissue growth alone." Rowe and Boyd on the basis of data of 77 women, "demonstrated that 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 reached in about 4 weeks. From this point on, during the last 6 lunar months there is a steady increase in the basal metabolic rate amounting to 13 per cent or more in excess of that conditioned by the gross increase in body weight."

Schwarz and Drabkin[17] attributed increased heat production to increased thyroid activity. This conclusion is based in part on the rise in blood iodine from the second (15.5 gamma per cent) to the tenth lunar month (22.5 gamma per cent) and dropping during the first two weeks of puerperium; in part on the observed hypertrophy of the anterior pituitary, with presumable increase of its thyrotropic activity during pregnancy; in part on the observed hypertrophy of the thyroid during pregnancy.

One of the most careful factual pictures of the course of energy metabolism during gestation on a normal woman is due to Root and Root.[18] "The course of the basal metabolism from the fifteenth week of pregnancy to the eighth week after delivery is reported in the case of primipara in whom pregnancy was uncomplicated by gain in adipose tissue or disease of any sort. The basal metabolic rate during the fourth month was essentially that predicted by the standard for non-pregnant women of the same age, height and weight. From this time, a steady increase in the total calories per twenty-four hours was observed until eleven days before delivery, when the total basal metabolism was 23 per cent. greater than that during the fourth

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[17] Schwarz, O. H., and Drabkin, C., Basal metabolic rates in late pregnancy and the puerperium. Am. J. Obst. and Gyn. *22*, 3, 1931. The work on the iodine was reported by O. Bokelmann and W. Scheringer, Arch. Gynakol., *143*, 512, 1931.

[18] Root, Howard F., and Root, Hester, K., The basal metabolism during pregnancy and the puerperium. Arch. Int. Med., *32*, 411, 1923.

month. This increase in metabolism is out of all proportion to the increase in basal metabolism shown by standard prediction tables for normal women with corresponding gain in weight. The gain in basal metabolism expressed as calories per kilogram from the fourth month of pregnancy to the eleventh day before delivery was 7.6 per cent. Following delivery, although subject's weight remained nearly stationary, the basal metabolism fell gradually to a point 9.6 per cent. lower than the rate observed during the fourth month of pregnancy.

"The high metabolic rate during the last month of pregnancy only partially reflects the much higher metabolic rate of the fetus per unit of weight since the maternal weight is made up in part of inactive tissues such as edema and the fluid contained in the amnion. It appears from our computations that the metabolism of the fetus at term was approximately 37 calories per kilogram, whereas the basal metabolism of the mother was 23.5 calories per kilogram during the fourth month of pregnancy and 22.1 calories per kilogram one month after delivery."

An advance report appeared[19] on basal energy and mineral metabolism on a young primipara for 66 days ante-partum and 62 days post-partum. "The rise in metabolism throughout the latter part of pregnancy does parallel strikingly the cumulative nitrogen and sulphur curves, and this fact constitutes an argument in favor of the concept that the increase is merely the result of increased protoplasmic mass. Since this concept must ignore a number of well-established glandular changes in pregnancy, or make the assumption that these have occurred without influencing the basal metabolism, and since the rise in metabolism is accompanied by a relative fall in the percentage of calories derived from protein, it is felt that a hormone influence responsible for the synthesis of a new mass of protoplasm must likewise be included in any explanation of the phenomenon that seemed complete."

Blackwood and Stirling[20] also believe that the syntheses involved in milk secretion are practically thermoneutral. Thus, for example, the heat of formation of 1 gm-mol. of lactose from 2 gm. mol. glucose is only about 5 calories, which is of course insignificant; and it is probable that the energy required for synthesis of protein and fat is no greater than that required for synthesis of lactose. "It is

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[19] Johnston, J. A., Hunscher, H. A., Hummel, F. C., Bates, M. F., Bonner, P., and Macy, I. G., The basal metabolism in pregnancy. The Wistar Institute Bibliographic Service, Advance abstract sheet, No. 302, March 15, 1938. Paper to appear in the J. Nutrition.

[20] Blackwood and Stirling, J. Biochem., *26*, 1127, 1932.

to be concluded therefore that the energy required for synthetic reaction by the mammary gland is so small as to be negligible.''

Graham[21] *et al.* investigated at the Missouri Station the energy expenditure of the mammary gland from data on: (1) blood-volume flow through the mammary gland and (2) respiratory exchange of the gland. It was this way found that the energy expended by the mammary gland in the goat is equivalent to 5-8% of the milk energy produced. This expense of course includes: (1) gland maintenance, and (2) conversion of milk precursors to milk. These two items can not be separated, but, according to these authors, it is reasonable to conclude from the small total energy expended by the mammary gland that the energy expense of converting *milk precursors* to milk is negligible.[22]

Murlin[23] published a classic investigation on pregnancy metabolism of a dog. Her heat production during sex rest was 505 Calories; 3 days before giving birth to 1 puppy, 551 Calories; 3 days before giving birth to 5 puppies, 765 Calories. In other words, the gestation metabolism above sex rest was 46 Calories for 1 puppy, and about 5 times (5.6 times) that much, 260 Calories, for 5 puppies.

Recently Pommerenke, Haney and Meek[24] investigated the energy metabolism of gestation and lactation in rabbits which confirm Murlin's results on the dog. The following table summarizes their data. (The weight data not given in this paper were sent to us by H. F. Haney; the column headed Cal./day was computed by us.)

		Heat Production		
Days Pregnant	Body Weight grams.	Cal./Day	Cal./Kg./hr.	Cal./Sq. M/hr.
1-10	2626	163	2.6	33.0
5-15	2583	163	2.6	33.3
11-20	2721	178	2.7	36.7
16-25	2765	193	2.9	37.8
21-30	3024	229	3.2	40.9
26-30	2795	214	3.2	41.5
Post Partum days				
1- 5	2522	200	3.3	37.2
1-10	2514	188	3.1	36.7
5-15	2663	187	2.9	34.8
11-20	2589	173	2.8	35.3
16-25	2539	162	2.7	33.6

The litter weights ranged from 110 to 490 gms., av. 295 gm. The young per litter ranged from 2 to 11, av. 6.6. The average heat production per litter of 8, 60.5 Cal./day, 196 Cal./Kg./Day, 2.5 Cal./hr., 8.2 Cal./Kg./hr.

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[21] Graham, W. R., Jr., Houchin, O. B., Peterson, V. E., and Turner, C. W., The efficiency of the mammary gland in the production of milk. Am. J. Physiology, 1938 (in press).

[22] It is interesting to note that the ratio of blood flow to milk flow in the *goats* investigated was between 150 and 250 parts to 1. The average O_2 content of arterial blood was 12.9%; of mammary blood 7.5%, so that the O_2 decrement was 5.3%. The CO_2 content of arterial blood was 46.4%, of mammary blood 53.2%, so that the CO_2 increment was 6.9%, and the apparent R. Q. about 1.3.

[23] Murlin, J. R., Am. J. Physiol. *23*, XXXII, 1908-9, see Lusk (l. c.) page 530 for a review of this investigation.

[24] Pommerenke, W. T., Haney, H. F., and Meek, W. J., The energy metabolism of pregnant rabbits. Am. J. Physiol., *93*, 249, 1930.

The above paper ends with the following conclusions: *1.* During pregnancy heat production increases from 2.6 to 3.2 Cal/kg./hr.; and from 32.7 to 41.5 Cal./sq. M./hr.; *2.* The total heat production of mother before parturition is about equal to that of mother and young combined after parturition; *3.* There is no increase in heat production per unit surface area of mother plus young.

The pregnancy-metabolism literature on large domestic animals will be discussed in a forthcoming paper.

2. **Lactation metabolism.**—The consensus of opinion on the influence of lactation on heat production is indicated by the following quotation from Lusk:[1] "It appears that lactation does not increase the heat production. This is not strange, since the arrangement of food materials in the preparation of milk depends upon hydrolytic cleavages and syntheses which involve hardly any thermal reactions."

While it may be true that no energy is involved in converting milk precursors into milk, the general metabolism of the animal might be expected to be higher during lactation because of: (1) higher maintenance of the hypertrophied active mammary gland; (2) higher metabolic level as a consequence of greater concentration of nutrients in blood called for milk production and greater food turn over; (3) increased level of endocrine activities.

Regarding the possible influence of hormones on metabolism, Graham[25] made the important contribution that thyroxine, one of the most prominent energy-metabolism activators, stimulates milk production; from which one might infer that the activity of the thyroid is increased during lactation. Such possibility was already noted in connection with the review of paper by Schwarz and Drabkin.

Graham demonstrated that removal of thyroids was followed by a rapid decline in milk production in dairy cattle. The milk production promptly rose on feeding thyroxin or dried thyroid gland to these cows. Moreover, when dried thyroid (about 2 oz. per day) was fed, or thyroxine injected (about 10 mg. per day) to normal cows during the declining phase of milk secretion (decline resulting from advancing stage of lactation), the milk and milk fat production increased considerably.

Graham's results on the stimulating influence of thyroid on production during the declining phase of lactation were amply confirmed.[26]

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[25] Graham, W. R., Jr., The effect of thyroidectomy and thyroid feeding on the milk secretion and milk fat production of cows. J. Nut. *7*, 407, 1934; The action of thyroxine on the milk and milk fat production of cows. Biochem. J. *38*, 1368, 1934.

[26] Jack, E. L., and Bechdel, S. I., A study of the influence of thyroxine on milk secretion.

Moreover, Reece and Turner[27] have indicated the presence of a tendency for a greater concentration of pituitary thyrotropic hormone during lactation than sex rest.

3. **Food consumption and physical activity during gestation and lactation.**—As noted in the introduction, the classic and only reference on feed consumption of dairy cattle during gestation is due to Eckles.[1] A brief review of Eckles' paper follows:

1. Six cows developed normal calves, made normal increases in body weight during gestation on a ration found by a six months trial to be only sufficient to maintain them at uniform weight when not pregnant or gestating.

2. This unexpected result may be due to: (1) better use of food during gestation (there was no increase in digestibility during gestation); (2) decreased maintenance during pregnancy (perhaps because the animals are quieter during gestation); (3) small amount of dry matter in fetus (new-born Jersey calf contains 73% water, placenta 85% water, amniotic fluid 95% water, dry matter in new-born calf 15-25 pounds equivalent to 110-170 pounds Jersey milk or 200-275 pounds Holstein Milk).

COMPOSITION OF CALVES FROM EXPERIMENTAL COWS

Weight of calf Pounds	Water Pounds	Dry Matter Pounds	Protein Pounds	Fat Lbs.	Ash Lbs.
75.0	54.8	20.2	14.2	2.5	3.2
48.5	35.4	13.1	9.2	1.6	2.1
95.0	69.4	25.6	18.0	3.2	4.0
82.5	60.3	22.2	15.6	2.8	3.5

COMPOSITION OF AMNIOTIC FLUID AND PACENTA (JERSEY)

	Amniotic fluid	Placenta
Weight—pounds	32.7	18.3
Water—per cent	95.9	85.6
Fat—per cent	0.92	0.92
Protein—per cent	3.36	12.20
Ash—per cent	0.65	0.89

TOTAL CONSTITUENTS PRODUCED BY COW IN AMNIOTIC FLUID BY PLACENTA

	Amniotic fluid	Placenta	Total
	Lbs.	Lbs.	Lbs.
Water	30.7	15.4	46.1
Dry matter	1.3	2.6	3.9
Fat	.03	.16	.19
Protein	1.07	2.19	3.26
Ash	.21	.16	.37

J. Dairy Sc., *18*, 195, 1935. Folley, S. J., and White, P., The effect of thyroxine on milk secretion and on the phosphatase of the blood and milk of the lactating cow. Proc. Roy. Soc. *120* B, 346, 1936. Herman, H. A., Graham, W. R., Jr., and Turner, C. W., The effect of thyroid and thyroxine on milk secretion in dairy cattle. Univ. Missouri Agri. Exp. Sta. Res. Bul. 275, 1938.

[27] Reece, R. P., and Turner, C. W., The lactogenic and thyrotropic hormone content of the pituitary gland. Mo. Agr. Exp. Sta. Res. Bul. 266, 1937.

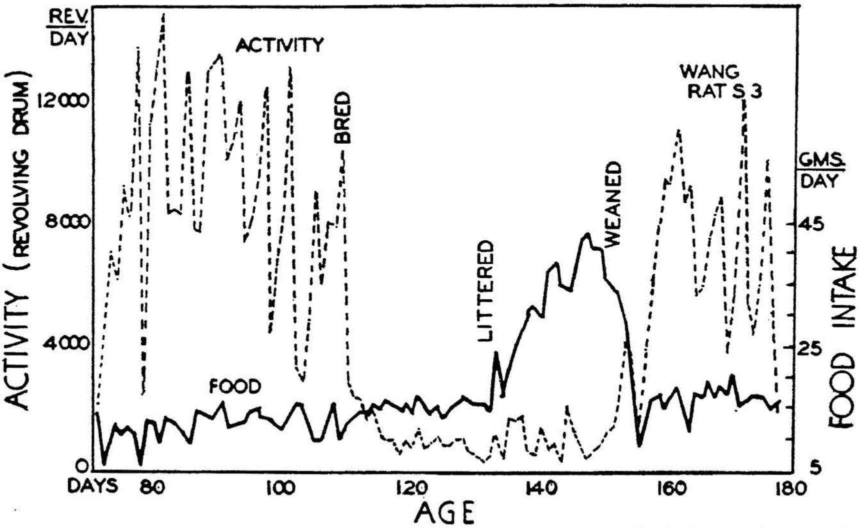

Fig. 12.—Activity and food consumption in rats during gestation, lactation, and sex rest, from Wang (Wang, G. H., The relation between "spontaneous" activity and oestrus cycle in the white rat. Comp. Psychol. Monographs, 2, No. 6, 1923).

Another important paper, due to Wang,[3] is concerned with food consumption and also with muscular activity of both lactation and gestation, but as it relates not to cows but to rats.

Wang's results on food consumption and physical activity during gestation and lactation are best represented by his curves, Figs. 2 and 12, and from the following abstracts and quotations.

1. During gestation there is no increase in food intake.

2. During lactation there is an enormous increase in food intake.

3. On weaning there is a quick return to the normal level of food intake.

4. There is a decrease in daily activity during pregnancy (and also during lactation). The nearer to the day of delivery the greater the decrease in activity. The average decrease in daily activity during the gestation period calculated as percentage of the average amount of daily activity for the 20 days before insemination, is about 90%.

5. The energy saved by the decrease in activity during pregnancy is probably used for the growth of the embryos and adnexa. This readjustment between muscular activity and growth makes it unnecessary to have an increase in daily food intake.

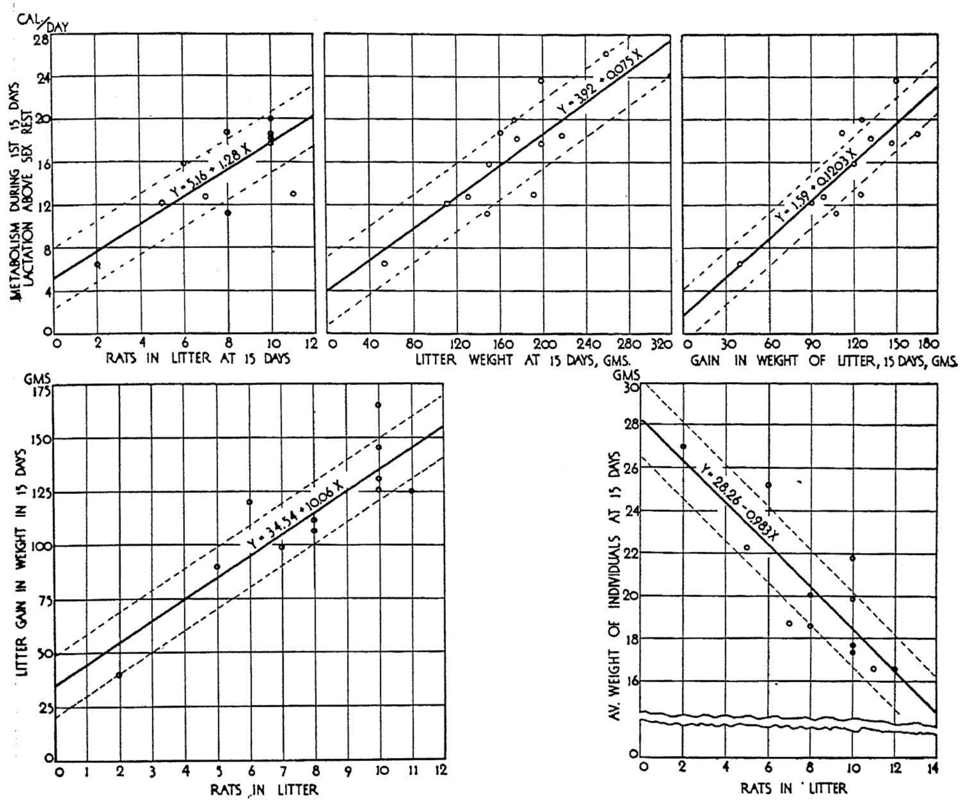

Fig. 13.—Interrelations between metabolism increment during lactation, litter size, and litter growth rate; also between growth rate of litter and of individuals and litter size.

Wang quotes Schick's observation that humans instinctively refrain from bodily activity during pregnancy, and this energy saving is used for meeting the increased demand for nourishment. The data by Macy and coworkers,[28] on food consumption of human mothers, which of course can not be as clear cut as those on rats or cows, confirm the aforecited results on animals.

Slonaker[2] published, simultaneously with Wang, an exhaustive study of the problem of food consumption and physical activity in rats during gestation and lactation. Slonaker's typical results, in their bearing on our problem, are summarized in the following conclusions:

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[28] Shukers, C. F., Macy, I. G., Donelson, E., Nimms, B., Hunscher, H. A., Food intake in pregnancy, lactation, and reproductive rest in the human mother. J. Nut. 4, 399, 1931. Coons, C. M., et al., Studies in metabolism during pregnancy. Okla. Agr. and Mec. Exp. Sta. Bul. 223, 1935.

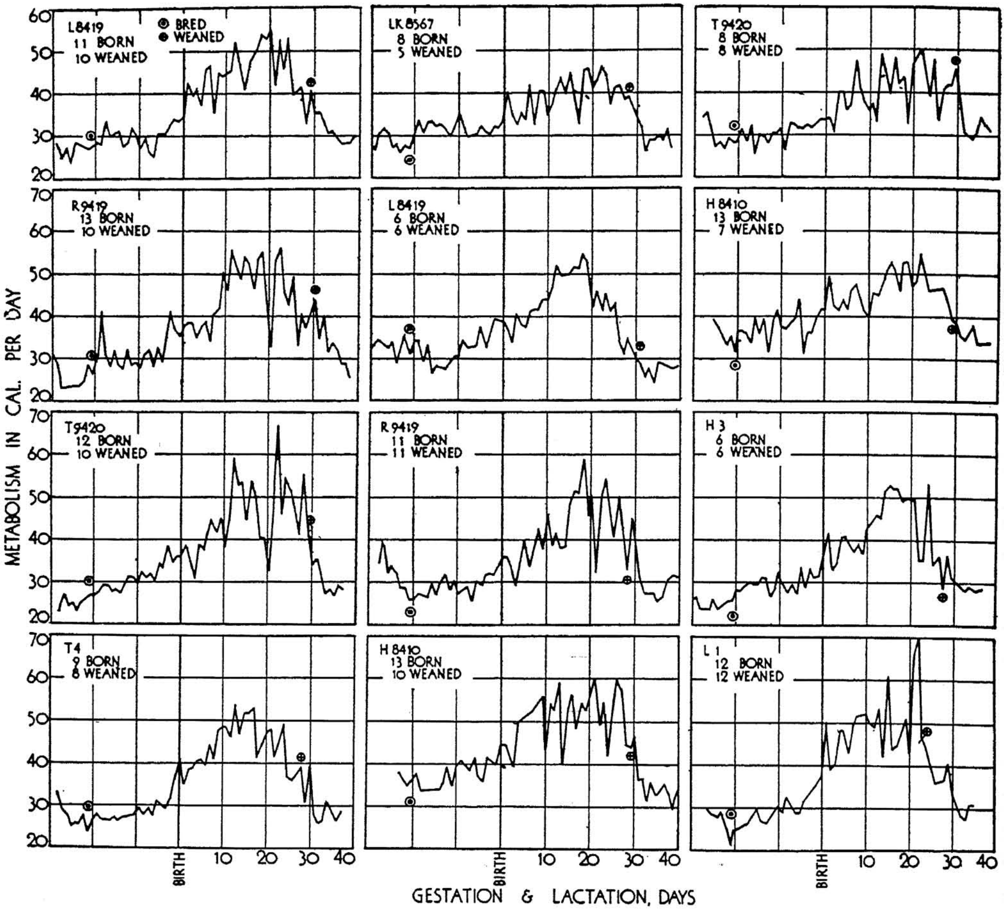
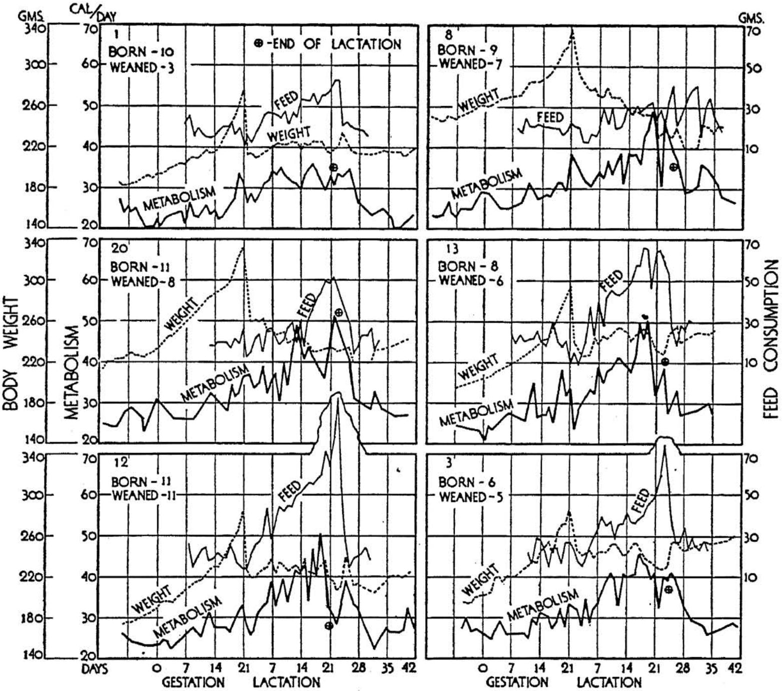


Fig. 14.—Additional metabolism data during gestation and lactation. See also chart on next page.

1. There is a characteristic drop in physical activity following conception. The daily activity dropped from 16,352 drum revolutions (in the exercising cage) preceding conception to 2779 revolutions following conception. The food consumption increased from an average of 18 grams per day during sex rest to only 20 grams during gestation.

2. During lactation, the physical activity is even below that of gestation, but food intake increased in proportion to litter size and to its growth rate (See Fig. 13).

In a personal communication (March 25, 1938) Professor Slonaker summarized his results thus: "I have found that both during gestation and pseudopregnancy there is an increase in weight and great reduction in activity accompanied by little change in food consumption. Apparently the energy which is usually used for activity is then used in growth."



See also Fig. 14 on opposite page.

C. ORIGINAL DATA FROM WHICH CHARTS WERE PLOTTED.

TABLE 1a. SOME METABOLISM DATA FOR RAT 9420 FOR FIGS. 3, 4, 5 AND 6.

2nd GESTATION AND LACTATION					3d GESTATION AND LACTATION					4th GESTATION AND LACTATION				
Day of Gestation Lactation	Body Weight gms.	Cal./Day	R. Q.	Dry Food[1] Intake Cals./Day	Day of Gestation Lactation	Body Weight gms.	Cal./Day	R. Q.	Dry Food Intake[1] Cals./Day	Day of Gestation Lactation	Body Weight gms.	Cal./Day	R. Q.	Dry Food Intake[1] Cals./Day
Gestation 1	219	26.9	0.95	(plus fresh milk *ad lib.* not included in total Cals.)	1	228	28.9	0.86	(plus fresh milk *ad lib.* not included in total Cals.)	1	252	35.0	0.83	(plus fresh milk *ad lib.* not included in food record)
2	225	27.9	0.98		2	235	31.6	0.88		2	246	...	0.77	
3	229	29.4	0.97		3	232	28.4	0.84		3	254	32.2	0.84	
4	229	29.0	0.96		4	235	32.3	0.94		4	260	33.1	0.87	
5	229	27.7	0.94		5	228	25.4	0.81		5	260	32.4	0.83	
6	233	28.7	0.96	....	6	241	30.4	0.96	....	6	262	33.3	0.81	....
7	234	27.6	0.84	....	7	238	29.8	0.88	....	7	261	31.4	0.79	....
8	238	29.5	0.97	....	8	242	28.0	0.93	....	8	262	36.5	0.81	....
9	240	31.4	0.96	....	9	242	30.8	0.86	....	9	256	29.8	0.71	....
10	247	31.1	1.01	....	10	243	30.1	0.85	....	10	263	33.8	0.80	....
11	246	29.5	0.96	....	11	249	31.7	0.90	....	11	265	31.0	0.80	....
12	249	32.8	1.01	....	12	247	26.3	0.81	....	12	271	32.1	0.81	....
13	250	31.2	1.00	....	13	252	33.3	0.95	....	13	271	32.0	0.89	....
14	254	32.2	0.91	....	14	257	33.1	0.95	46.4	14	273	30.6	0.86	....
15	261	30.1	1.04	....	15	262	31.9	0.93	43.2	15	278	34.1	0.88	73.6
16	267	34.8	0.86	....	16	269	31.5	0.93	49.6	16	285	35.5	0.86	67.2
17	276	33.5	0.95	48.0	17	273	32.6	0.92	46.4	17	287	35.9	0.79	67.2
18	285	38.5	0.86	54.4	18	281	31.6	0.83	59.2	18	298	34.7	0.78	64.0
19	300	34.5	1.10	51.2	19**	281	32.6	0.74	12.8	19	302	34.5	0.81	57.6
20	314	36.2	0.78	51.2	20	296	33.6	0.93	62.4	20	295	34.7	0.73	25.6
21	315	36.2	0.88	44.8	21	302	33.8	0.85	35.2	21	...	...	...	12.8
Lactation 1*	247	39.0	0.82	25.6	1*	256	34.3	0.80	32.0	1*	233	33.9	0.74	12.8
2	240	35.9	0.87	35.2	2	252	30.8	0.92	33.6	2	228	33.0	0.75	44.8
3	242	30.8	0.87	38.4	3	255	40.0	0.97	43.2	3	232	36.9	0.75	73.6
4	247	39.0	1.09	51.2	4	252	40.0	0.80	48.0	4	237	35.8	0.83	70.4
5	247	37.4	0.97	51.2	5	247	35.9	0.75	35.2	5	249	42.6	0.84	92.8
6	245	42.1	1.06	70.4	6	252	37.8	1.01	73.6	6	259	42.1	0.84	102.4
7	247	42.4	1.12	57.6	7	262	47.8	1.12	80.0	7	257	40.4	0.83	86.4
8	246	41.7	0.97	60.8	8	258	40.9	0.92	72.0	8	252	39.2	0.82	80.[illegible]
9	252	45.2	1.25	80.0	9	259	37.8	1.01	83.2	9	259	38.4	0.81	96.0

10	246	38.0	1.13	86.4
11	251	44.8	1.11	80.0
12	250	59.3	0.91	96.0
13	246	52.9	0.87	96.0
14	257	53.7	1.20	102.4
15	246	44.5	1.03	108.8
16	251	54.1	1.19	99.2
17	225	49.5	0.83	83.2
18	234	40.1	1.05	86.4
19	230	40.1	1.05	....
20	231	32.5	0.82	....
21	234	47.7	1.13	....
22	240	66.9	1.18	....
23	237	46.3	1.16	....
24	238	54.1	1.15	....
25	238	46.7	1.20	....
26	No record			
27	236	41.3	0.97	....
28	243	52.4	0.95	....
29	236	42.6	1.15	....
Post Lactation 1	242	34.4	0.98	....
2	232	35.9	0.91	....
3	225	31.7	0.99	....
4	220	27.2	0.87	....
5	220	28.5	0.93	....
6	211	26.6	0.74	....
7	224	29.6	0.92	....
8	226	28.4	1.00	....

*Littered 12 rats.

10	258	35.9	0.89	81.6
11	255	37.6	0.90	75.2
12**	242	33.4	0.74	35.2
13	251	49.1	1.07	86.4
14	258	44.0	1.14	92.8
15	252	39.8	1.14	81.6
16	257	48.3	1.12	99.2
17	251	42.1	1.01	99.2
18	251	43.8	0.95	131.2
19	232	32.3	0.74	....
20	245	46.9	1.14	....
21	247	48.7	1.12	....
22	251	50.5	1.13	....
23	252	44.9	1.00	....
24	245	39.0	1.03	....
25	248	48.0	1.07	....
26**	230	32.5	0.76	....
27	235	41.1	1.07	....
28	245	42.1	1.15	....
29	244	41.9	1.07	....
30	250	46.4	0.95	....
1	...	...	...	....
2	230	30.6	0.85	....
3	231	30.0	0.94	....
4	229	29.3	0.81	....
5	235	31.3	0.86	....
6	239	34.7	0.87	....
7	245	326	0.82	....
8	250	31.3	0.95	....

*Littered 8 rats.

**Basal value.

[1] Diet 798 + Fresh Whole Milk *ad lib.* milk calories not included in total.
1 gram of this ration is equivalent to 3.2 Cal. TDN.

10	267	40.4	0.80	94.4
11	260	39.5	0.80	73.6
12	257	35.5	0.78	80.0
13	261	40.6	0.80	108.8
14	264	39.0	0.85	94.4
15	264	38.8	0.86	102.4
16	266	40.1	0.84	94.4
17	262	36.4	0.84	83.2
18	262	38.6	0.89	92.8
19	254	35.7	0.80	....
20	257	35.7	0.87	....
21	257	36.8	0.89	....
22	269	40.2	0.87	....
23	269	38.5	0.85	....
24	270	37.8	0.88	....
25	262	40.0	0.81	....
26	263	37.8	0.84	....
27	253	32.0	0.86	....
28	260	36.1	0.85	....
29	258	35.5	0.89	....

*Littered 11 rats.

TABLE 1b. SOME METABOLISM DATA FOR RAT 9419

2nd GESTATION AND LACTATION

Day of Gestation Lactation	Body Weight gms.	Cal./Day	R. Q.	Dry Food Intake[1] Cal./Day of TDN (plus fresh milk *ad lib.* not included in total Cals.)
1	202	29.9	0.84	
2	205	41.6	0.99	
3	207	30.7	0.79	
4	210	28.4	0.93	
5	213	32.9	0.91	
6	214	28.7	0.91	
7	216	27.6	0.94	....
8	219	32.2	0.91	....
9	220	28.6	0.87	....
10	225	29.3	0.85	....
11	228	28.0	0.94	....
12	231	31.2	0.91	....
13	238	32.5	0.98	....
14	237	28.3	0.99	....
15	246	33.0	0.97	....
16	248	29.5	0.90	....
17	258	35.8	0.87	44.8
18	268	41.3	0.81	48.0
19	278	37.0	0.85	32.0
20	281	35.2	0.86	32.0
21	295	37.6	0.91	38.4
1*	224	38.6	0.80	60.8
2	218	38.5	0.72	25.6
3	225	34.8	1.03	41.6
4	228	37.6	1.01	60.8
5	231	38.9	1.06	60.8
6	231	34.0	1.14	73.6
7	230	40.5	1.10	80.0

3d GESTATION AND LACTATION

Day of Gestation Lactation	Body Weight gms.	Cal./Day	R. Q.	Dry Food Intake Cal./Day of TDN (plus fresh milk *ad lib.* not included in Cals.)
1	216	26.0	0.94	
2	218	27.4	0.83	
3	222	27.1	0.91	
4	225	26.5	0.90	
5	227	29.7	0.82	
6	227	27.0	0.88	....
7	231	32.1	0.87	....
8	236	31.9	0.87	....
9	236	28.0	0.87	....
10	238	30.5	0.97	40.0
11	243	27.7	0.92	35.2
12	244	28.4	0.85	36.8
13	248	28.7	0.86	44.8
14**	243	25.2	0.79	19.2
15	251	30.4	0.81	46.4
16	261	29.3	0.94	38.4
17	272	31.8	0.97	40.0
18	280	32.2	0.89	41.6
19	288	31.8	0.88	43.2
20	296	33.6	0.81	41.6
21**	295	36.4	0.73	11.2
1*	244	35.8	0.78	43.2
2	239	33.9	0.82	28.8
3	238	29.0	0.85	41.6
4	246	35.6	0.97	54.4
5	242	40.0	0.78	49.6
6	244	33.7	0.84	64.0
7**	243	37.7	0.78	51.2

4th GESTATION AND LACTATION

Day of Gestation Lactation	Body Weight gms.	Cal./Day	R. Q.	Dry Food Intake Cal./Day of TDN (plus fresh milk *ad lib* not included in total Cals.)
1	244	34.0	0.80	
2**	238	27.0	0.77	
3	245	33.6	0.79	
4	251	31.5	0.88	
5	255	31.2	0.86	
6	258	31.1	0.82	
7	259	30.5	0.85	....
8	260	31.2	0.83	....
9**	254	29.1	0.72	....
10	260	30.0	0.77	....
11	268	30.1	0.80	....
12	271	30.6	0.79	....
13	274	32.4	0.86	....
14	276	33.6	0.84	....
15	276	35.1	0.79	89.6
16	281	34.3	0.82	70.4
17	281	34.6	0.83	89.6
18	286	32.8	0.83	73.6
19	292	32.5	0.78	83.2
20	295	33.7	0.78	70.4
21	...	...	...	70.4
1*	283	39.7	0.74	92.8
2	279	39.8	0.79	48.0
3	275	36.2	0.82	64.0
4	275	40.7	0.80	60.8
5	280	39.0	0.81	86.4
6	279	36.3	0.83	70[illegible]
7	284	37.4	0.84	89.6

8	2[illegible]8	42.0	1.07	76.8
9	233	50.2	1.19	102.4
10	237	46.1	1.16	96.0
11	240	55.8	1.22	99.2
12	237	52.3	1.25	102.4
13	237	48.1	1.20	112.0
14	239	54.1	1.28	86.4
15	236	52.3	1.21	105.6
16	231	46.1	1.21	124.8
17	237	53.6	1.25	89.6
18	226	50.7	1.15	96.0
19	222	45.5	1.10	....
20	216	32.9	1.00	....
21	225	53.0	1.16	....
22	228	56.0	1.29	....
23	229	45.6	1.12	....
24	224	42.4	1.10	....
25	219	49.2	1.18	....
26	215	33.1	1.07	....
27	220	40.8	1.08	....
28	220	37.5	1.08	....
29	No record			....
30	219	44.0	1.15	....
1	217	34.6	1.03	....
2	221	40.3	0.86	....
3	208	31.9	0.91	....
4	205	33.7	0.80	....
5	211	32.2	0.93	....
6	210	28.8	0.88	....
7	208	28.6	0.89	....
8	211	25.7	0.84	....

*Littered 13 rats.

[1]Diet 798 + 1 gram of this ration is equivalent to 3.2 Calories of TDN.

8	253	42.7	1.06	100.8
9	255	37.9	1.03	88.0
10	256	45.5	1.06	100.8
11	261	38.5	1.16	99.2
12	251	41.7	0.81	96.0
13	251	37.9	0.86	123.2
14***	230	38.5	0.73	52.8
15	239	48.8	0.91	118.4
16	246	51.6	1.12	105.6
17	247	50.7	1.14	....
18	248	58.9	1.16	121.6
19	239	45.3	1.01	....
20	236	51.6	1.05	....
21**	220	32.9	0.83	....
22	230	50.0	1.16	....
23	238	54.5	1.16	....
24	237	...	1.03	....
25	235	40.5	1.01	....
26	238	50.4	1.22	....
27	236	40.4	1.08	....
28	215	32.7	0.76	....
1	230	46.4	1.21	....
2	244	39.4	0.98	....
3	230	32.1	1.07	....
4	219	27.6	0.92	....
5	...	...	...	....
6	221	27.7	0.86	....
7	224	25.6	0.93	....
8**	218	27.1	0.76	Milk diet
9	229	30.8	0.84	....
10	234	32.4	0.86	....
11	237	29.0	0.84	....
12	239	29.3	0.82	....

*Littered 11 rats.

**15-hour basal value.

***14-hour basal value.

8	285	39.2	0.87	89.6
9	279	35.3	0.76	104.0
10	285	39.4	0.87	91.2
11	282	37.9	0.83	76.8
12	279	36.1	0.85	104.0
13	277	38.6	0.82	99.2
14	278	34.4	0.85	94.4
15	279	36.8	0.80	97.6
16	275	46.2	0.88	99.2
17	276	43.8	0.88	104.0
18	...	...	...	104.0
19	...	...	...	....
20	277	38.4	0.87	....
21	278	36.9	0.90	....
22	286	46.5	0.85	....
23	291	51.6	0.85	....
24	286	42.6	0.89	....
25	289	49.4	0.85	....
26	286	40.6	0.92	....
27	284	42.8	0.86	....
28	274	46.0	0.83	....
29	273	42.8	0.86	....

*Littered 3 rats.

**14-hour basal value.

TABLE 2. METABOLISM DATA ON RAT 1032 AND HER LITTER FOR FIGS. 8a AND 8b
(7 young, fast began age 11 days, 11/13/38)

	Hours Fast (approx.)	Body Weight gms.		Metabolism Cal./Day		O_2 Consumed Gm./Day		CO_2 Produced Gms./Day		R. Q.		"Milk Yield" Gms.	Food Consumed by Mother gms.	Loss in body weight while in respiration chamber Gms./Hour		Mid-* time of Record	Duration of Record Minutes
	Mother	Mother	Litter	Mother	Litter	Mother	Litter	Mother	Litter	Mother	Litter			Mother	Litter		
1.	—21	245.1	103.6	37.3	42.8	10.25	12.98	15.48	13.01	1.098	.728	+2.8	2.6	4.65	.55	4:01 p.m.	120
2.	—17	248.6	104.0	43.9	39.6	12.47	11.94	16.94	12.11	.988	.737	+3.1	4.7	2.65	.45	7:47	120
3.	—13	246.5	105.8	43.3	41.9	12.05	12.60	17.06	12.91	1.029	.745	+2.7	2.5	2.75	.65	11:34	120
4.	— 6	236.7	108.0	40.1	32.0	11.39	9.64	15.23	9.88	.972	.745	+3.0	6.5	3.30	.60	6:53 a.m.	120
5.	1	235.4	110.5	40.1	36.4	11.08	10.99	16.31	11.06	1.070	.731	+3.1	Fast	1.15	.45	2:19 p.m.	120
6.	5	226.3	112.9	40.2	34.4	12.13	10.43	12.54	10.85	.752	.756	+0.5	"	3.35	.50	5:55	120
7.	8	220.7	112.3	34.8	38.2	10.43	11.54	10.97	11.69	.765	.736	0.0	"	.75	.45	9:09	120
8.	12	217.0	111.1	37.2	37.0	11.18	11.14	11.63	11.22	.754	.733	—0.5	"	2.05	.30	12:54 a.m.	120
9.	16	213.0	109.7	31.4	23.8	9.55	7.25	9.37	7.12	.713	.714	—0.6	"	.55	.19	5:22	240
10.	21	209.7	108.7	32.0	19.6	9.67	5.96	8.62	5.87	.738	.714	—0.6	"	.70	.30	9:43	120
11.	24	206.6	107.4	28.9	15.4	8.76	4.78	8.71	4.42	.723	.677	—0.5	"	.50	.25	12:50 p.m.	120
12.	27	204.0	106.2	26.3	16.9	7.94	5.12	8.04	5.10	.736	.723	—0.3	"	.50	.20	4:21	120
13.	32	201.2	105.2	30.0	19.7	9.14	5.96	8.94	5.98	.711	.728	—0.2	"	.85	.35	8:37	120
14.	35	199.6	104.2	28.4	19.9	8.65	6.02	8.46	5.98	.711	.721	—0.4	"	.45	.30	11:57	120
15.	39	196.9	103.0	25.6	17.5	7.76	5.33	7.64	5.20	.715	.712	—0.5	"	.28	.28	3:42 a.m.	240
16.	45	193.9	100.9	22.2	17.8	7.08	5.42	7.12	5.23	.778	.702	—0.4	"	.92	.28	10:23	240
17.	51	189.5	99.1	25.8	19.3	7.84	5.87	7.72	5.76	.716	.714	—0.7	"	.25	.28	3:48 p.m.	240
18.	56	187.1	97.6	23.7	24.6	7.16	7.43	7.22	7.44	.733	.731	—0.6	"	.58	.32	9:00	240
19.	62	183.8	95.4	25.9	22.9	7.85	6.98	7.88	6.86	.730	.714	—0.4	"	.50	.45	2:36 a.m.	300
20.	66	182.5	93.9	22.3	17.2	6.74	5.23	6.83	5.09	.736	.707	—0.4	"	.10	.25	6:58	120
21.	71	180.0	92.8	20.9	15.1	6.33	4.54	6.35	4.76	.729	.764	—0.5	"	.62	.45	12:21 p.m.	300
22.	76	177.8	91.6	22.4	18.2	6.84	5.48	6.62	5.62	.704	.744	—0.6	"	.00	.20	4:48	120
23.	80	176.8	90.3	20.6	14.2	6.26	4.33	6.27	4.25	.728	.714	—0.5	"	.25	.32	8:54	240
24.	85	176.6	88.7	19.7	14.4	5.95	4.40	6.07	4.27	.741	.706	—0.8	"	.00	.17	2:00 a.m.	240
25.	90	174.5	86.9	18.1	10.4	5.48	2.95	5.35	3.17	.741	.727	—0.5	"	.70	..	7:00	120
26.	96	171.7	75.8	18.8	9.1	5.67	2.75	5.74	2.77	.736	.734	—0.3	"	.48	..	12:42 p.m.	300
27.	100	168.4	64.7	20.4	9.5	6.17	2.98	6.07	2.69	.715	.656	—0.4	"	1.20	..	5:22 p.m.	120
28.	104	162.3	61.9	18.9	9.0	5.70	2.69	5.89	2.81	.751	.759	—0.6	"	.05	..	9:22	240
29.	127	159.8	....	19.4	....	5.06	....	5.57	....	.684	...	....	"	...	..	8:15	180
30.	130	159.6	....	15.1	....	4.40	....	4.73	....	.752	...	....	"	...	..	10:45	120
31.	133	159.0	....	15.0	....	4.16	....	4.60	....	.739	...	....	"	...	..	2:15 a.m.	300
32.	137	158.6	....	11.1	....	3.28	....	3.75	....	.832	...	....	"	...	..	6:15	180
33.	141	157.9	....	11.0	....	3.25	....	3.68	....	.822	...	....	"	...	..	9:45	240
34.	169	148.0	....	10.2	....	3.03	....	3.39	....	.814	...	....	"	...	..	2:15 p.m.	300

*Since both mother and litter records were secured as nearly as possible at the same time the mid-time time of the mother was used in plotting both mother and litter data. (See note on following page.)

Explanatory notes for Table 2. For *methods* of measuring metabolism and R. Q., see Missouri Agric. Exp. Sta. Res. Bul. 274, Feb. 1938 (entitled "Diurnal metabolic and activity rhythms"). The initial *weight of mother rat,* 235.4 gms.; final weight (7 days, or 170 hours fast), 148 gms.; loss 87.4 gms. about 37%. She recovered to normality. Initial *weight of litter* of 7, 110.5 gms.; weight after 95 hours of fast in mother, 86.9 gms. (1st death occurred at this time); weight loss, 23.6 gms., about 22%. Mother had access to water; litter could of course get no water when lactation ceased. *"Milk yield"* was gauged by gain in body weight during a suckling period of 45 minutes. Of course the body weight loss (insensible perspiration) during the 45 minutes of maintenance must be added. Thus if body weight gain during 45-minute suckling is 3.0 gms., and if 45-minute sterile suckling results in a weight loss of 0.7 gm., then the "milk yield" is 3.7 gms. We did *not* make such corrections, but merely defined the term "milk yield." The animals usually spent 2-hour periods in the respiration chamber, and *metabolism time* refers to the midpoint of the 2-hour interval. The mother received diet 798 composed of yellow corn 76; linseed meal 16; casein "75", 5; alfalfa meal, 2. According to Henry and Morrison's tables, this mix contained 80.6% TDN, so that 1 gram of the food contained 0.81 gm. TDN. Assuming 1 gm. TDN has a fuel value of 4 Cal., then 1 gm. food contains 3.2 Cal. The mother consumed about 20 gms. of this mix, or 64 Cal. TDN a day, plus liquid whole milk ad libitum of which no record was kept. The *laboratory temperature* ranged from 27.5-29° C, mostly 28°.

TABLE 3. METABOLISM DATA FOR FIGS. 9a AND 9b.

METABOLISM DATA ON RAT 1041 AND HER LITTER

(7 young, fast began age 10 days, 11/20/37)

Hours Fast (approx.) Mother	Body Weight gms.		Metabolism cal./day		O_2 Consumed gms./day		CO_2 Produced gms./day		R. Q.		"Milk Yield"[3] gms.	Food Consumption of Mother[2] gms.	Loss in body weight while in respiration chamber gms.		Mid Time of Record[1]	Duration of Respiration Chamber Record minutes
	Mother	Litter	Mother	Litter	Mother	Litter	Mother	Litter	Mother	Litter			Mother	Litter		
—14 hrs., 56 min.	282.3	87.0	47.0	29.8	13.50	8.99	17.28	9.07	.931	.733	+1.3	1.4	5.5	0.9	3:16 p.m.	90
—11 " 40 "	275.5	86.9	46.0	.31.7	13.20	9.55	16.94	9.83	.933	.748	+1.8	4.6	2.8	0.3	6:32	120
— 8 " 16 "	274.6	87.8	46.3	30.1	12.68	9.05	18.61	9.43	1.066	.758	+3.2	1.9	1.0	0.4	9:56	120
— 2 " 23 "	268.7	90.2	46.9	33.0	13.44	9.95	17.64	10.24	.954	.748	+2.0	4.4	1.8	0.4	1:19 a.m.	120
Fast 1 hr.	270.6	90.6	49.4	27.0	14.24	8.15	17.95	8.27	.916	.738	+2.7	Fast started	1.4	0.2	7:12	120
3 hrs., 58 min.	264.1	92.4	40.0	28.6	11.90	8.64	13.46	8.59	.822	.723	+1.7	"	1.5	1.4	10:10	120
6 " 43 "	259.6	92.4	37.2	27.8	11.12	8.42	11.90	8.47	.778	.731	+1.6	"	2.3	0.5	12:55 p.m.	120
9 " 35 "	255.3	93.1	35.2	30.1	10.56	9.11	11.15	9.18	.768	.733	+1.2	"	0.2	0.5	3:47	120
12 " 27 "	252.1	92.8	40.7	29.6	12.24	8.95	12.64	9.00	.750	.731	+1.0	"	1.4	0.8	6:39	120
15 " 3 "	248.1	93.1	36.8	32.8	11.12	9.86	11.25	10.29	.736	.759	0.0	"	0.5	0.5	9:15	90
17 " 38 "	246.0	92.4	38.2	32.3	11.52	9.80	11.59	9.65	.731	.715	—0.5	"	0.3	0.3	11:50	120
Feed 1 " 0 "	245.1	91.4	38.5	25.8	11.61	7.78	11.84	7.93	.742	.741	—0.6	5.1	0.1	0.2	3:25 a.m.	180
4 " 50 "	249.2	90.4	48.1	10.3	14.52	3.11	14.75	3.16	.739	.738	+0.6	6.2	0.8	0.2	7:15	120
8 " 46 "	262.5	90.5	38.7	10.6	10.92	3.22	15.24	3.21	1.016	.725	+0.9	1.0	1.1	0.2	11:11	155
12 " 17 "	260.2	90.6	38.4	12.3	10.82	3.75	15.07	3.66	1.012	.709	+2.2	5.2	0.7	0.4	2:42 p.m.	190
19 " 32 "	257.6	96.5	43.4	31.1	11.88	9.41	17.47	9.50	1.069	.734	+1.9	4.3	1.0	0.4	9:57	120
RAT 1309-0 AND HER LITTER (6 young,* fast began age 9 days, 1/14/38)																
—19 hrs., 16 min.	268.1	61.6	45.6	24.7	13.12	7.46	16.84	7.66	.933	.746	1.2	0.9	0.8	1.1	1:40 a.m.	120
—15 " 56 "	262.7	61.6	41.3	25.8	11.88	7.76	15.36	7.96	.940	.745	1.0	5.3	1.7	0.5	5:00	120
— 6 " 22 "	258.2	65.7	39.0	26.8	11.04	8.08	15.18	8.38	1.000	.754	1.4	0.2	1.8	0.4	2:34 p.m.	120
— 2 " 52 "	262.2	56.3	43.1	27.8	11.52	7.22	14.52	7.40	.917	.745	2.6	3.3	1.7	0.4	6:04	120
Fast 1 hr.	256.2	57.6	40.1	23.2	11.47	7.04	15.00	7.10	.950	.734	2.0	Fast started	1.7	0.5	9:56	120
3 hrs., 57 min.	248.8	58.8	44.3	24.6	12.82	7.40	15.76	7.68	.893	.754	0.7	"	3.2	0.4	12:53 a.m.	120
7 " 49 "	242.0	57.0	37.0	23.6	10.91	7.11	12.53	7.29	.835	.745	3.7	"	0.6	0.4	4:45	240
12 " 24 "	234.1	59.5	35.2	23.5	10.54	7.12	11.18	7.15	.771	.731	0.0	"	2.8	0.5	9:20	120
14 " 36 "	229.9	58.4	30.2	21.1	9.12	6.36	9.40	6.44	.749	.736	—0.5	"	0.1	0.6	12:32 p.m.	120
19 " 46 "	230.0	57.1	29.2	20.2	8.76	6.11	9.10	6.11	.755	.727	—0.2	"	0.4	0.3	3:42	120
23 " 49 "	227.2	56.1	29.6	15.6	8.93	4.69	9.15	4.81	.744	.744	0.0	"	0.8	0.3	7:45	240
27 " 47 "	224.0	55.4	33.4	17.2	10.12	5.21	10.21	5.08	.734	.708	—0.3	"	1.1	0.2	11:43	120
29 " 35 "	223.1	54.7	33.6	15.4	10.20	4.69	9.92	4.57	.707	.709	—0.2	"	0.5	0.3	2:31 a.m.	120
32 " 45 "	218.1	54.7	31.8	12.5	9.67	3.76	9.56	3.83	.719	.741	—0.6	"	1.6	0.0	8:31	120
Feed 1 " 0 "	215.5	53.5	29.6	11.9	9.02	3.65	8.92	3.48	.718	.694	—0.4	3.2	0.5	0.1	11:41	120
4 " 25 "	228.1	52.9	34.0	12.0	10.21	3.65	10.63	3.47	.757	.691	+0.9	1.6	0.4	0.1	3:06 p.m.	120
7 " 49 "	237.2	53.1	32.0	11.8	9.37	3.58	11.17	3.60	.867	.732	+1.1	2.2	0.3	0.1	6:30	120
11 " 24 "	241.7	53.7	34.0	14.2	9.72	4.30	12.67	4.18	.948	.707	+2.0	7.7	0.1	0.1	10:05	120
23 " 42 "	288.3	49.1	33.8	12.6	9.65	3.79	12.88	3.84	.971	.736	+1.2	3.9	0.4	0.1	10:23 a.m.	120

RAT 1022 AND HER LITTER

(5 young, fast began age 10 days, 12/8/37)

—15 hrs., 7 min.	271.5	51.5.	40.2	19.3	11.38	5.87	15.72	5.83	1.005	.723	+1.8	2.3	0.5	0.8	12:30 a.m.	120
—11 " 53 "	268.2	52.3	41.4	22.0	11.66	6.62	16.30	6.74	1.016	.740	+1.4	2.7	1.8	0.2	3:44 a.m.	120
— 5 " 38 "	264.2	53.3	37.1	21.6	10.64	6.55	13.73	6.54	.938	.725	+1.3	2.2	0.8	0.3	9:59 a.m.	120
— 2 " 35 "	262.1	53.7	36.5	23.3	10.38	7.07	13.99	7.03	.980	.723	+1.7	1.5	0.4	0.3	1:02 p.m.	120
Fast 1 hour	259.0	54.7	35.3	22.3	10.25	6.73	12.76	6.77	.905	.731	+0.9	Fast started	1.0	0.1	4:37 p.m.	120
3 hrs., 51 min.	253.7	55.0	34.0	21.5	10.06	6.47	11.41	6.66	.825	.749	+1.3	"	1.9	0.2	7:28 p.m.	120
6 " 42 "	249.7	55.9	36.5	24.0	11.02	7.32	11.44	7.10	.755	.706	+0.3	"	0.3	0.2	10:19 p.m.	120
9 " 41 "	246.5	55.0	37.8	22.0	11.36	6.62	11.88	6.66	.760	.730	0.0	"	1.0	0.6	1:18 a.m.	120
13 " 43 "	243.7	54.1	36.2	19.7	10.87	5.96	11.39	5.97	.762	.728	+0.3	"	0.9	0.1	5:20 a.m.	205
17 " 33 "	240.5	53.8	31.8	15.8	9.58	4.79	9.91	4.92	.752	.747	—0.3	"	0.5	0.4	9:10 a.m.	120
20 " 20 "	239.2	53.0	28.1	12.7	8.44	3.85	8.80	3.83	.758	.723	+0.4	"	0.3	0.2	11:57 a.m.	120
25 " 20 "	235.5	53.1	30.1	11.4	9.14	3.44	9.15	3.42	.728	.723	+0.5	"	1.0	0.1	4:57 p.m.	180
29 " 0 "	231.7	53.3	36.8	13.0	11.12	4.06	11.18	4.37	.731	.783	—0.3	"	0.3	0.1	8:37 p.m.	120
Feed 1 " 0 "	230.0	52.9	33.8	10.6	10.23	3.22	10.22	3.19	.726	.722	—0.5	4.0	0.3	0.0	12:05 a.m.	180
6 " 3 "	234.5	51.8	36.7	7.2	10.70	2.20	12.89	2.09	.876	.690	+1.0	3.5	0.3	0.2	5:08 a.m.	180
10 " 25 "	237.0	52.4	33.7	6.7	9.62	1.98	12.61	2.29	.952	.842	+1.2	3.9	0.0	0.0	9:30 a.m.	180
15 " 50 "	240.5	54.2	32.4	11.9	9.14	3.59	12.77	3.64	1.016	.736	+1.2	1.8	0.6	0.2	2:55 p.m.	180
19 " 5 "	241.7	54.7	36.0	15.2	10.19	4.64	14.00	4.52	.999	.708	+2.3	3.5	1.8	0.3	6:10 p.m.	120
22 " 17 "	240.7	56.2	31.0	18.5	8.69	5.56	12.24	5.86	1.024	.766	+1.1	3.6	0.8	0.3	9:22 p.m.	120

RAT 239 HT AND HER LITTER

(7 young, fast began age 10 days, 1/14/38)

	255.4	86.7	47.8	34.2	13.55	10.36	18.31	10.44	.983	.733	1.7	5.7	1.7	0.7	1:25 a.m.	120
—18 hrs., 22 min.	255.6	86.5	43.6	30.7	12.26	9.28	17.09	9.38	1.013	.736	2.8	4.3	1.2	0.6	4:50	120
—14 " 57 "	245.6	91.0	37.4	33.0	10.97	10.03	13.06	10.04	.865	.728	1.4	1.8	0.5	0.5	2:22 p.m.	120
— 6 " 25 "	245.8	91.7	43.0	31.9	12.41	9.62	15.73	9.84	.923	.744	1.5	4.7	0.7	0.1	5:48	120
Fast 1 hour	243.7	92.2	38.2	31.3	10.79	9.47	14.83	9.42	1.000	.723	0.7	Fast started	1.3	0.7	9:47	120
3 hrs., 55 min.	240.3	91.9	30.7	30.2	9.06	9.17	10.54	9.19	.846	.729	1.4	"	0.3	0.4	12:42 a.m.	120
7 " 48 "	233.0	91.9	33.0	23.6	9.80	7.14	10.87	7.27	.806	.740	3.4	"	2.1	1.0	4:35	240
12 " 11 "	226.6	93.6	37.4	21.0	11.28	6.34	11.68	6.37	.752	.731	—0.1	"	0.9	0.7	8:58	120
16 " 28 "	224.9	92.3	28.8	19.7	8.56	5.95	9.43	5.95	.801	.727	—0.6	"	0.1	0.6	12:15 p.m.	120
19 " 20 "	225.3	90.9	27.8	18.1	9.02	5.51	9.12	5.48	.800	.724	—0.4	"	1.0	0.3	3:27	120
23 " 48 "	222.5	89.6	28.4	17.6	8.50	5.35	9.04	5.33	.773	.724	—0.0	"	1.0	0.7	7:35	240
27 " 43 "	219.9	88.8	31.0	16.0	9.31	4.85	9.61	4.81	.750	.722	—0.8	"	0.1	0.2	11:30	120
30 " 36 "	219.5	87.5	32.2	14.0	9.68	4.30	9.85	4.04	.739	.684	—0.2	"	0.4	0.3	2:23 a.m.	120
Feed 1 " 0 "	215.9	86.9	26.9	12.6	8.15	3.80	8.12	3.82	.725	.729	0.0	3.8	1.4	0.2	8:21	120
4 " 7 "	212.4	86.5	31.2	14.0	9.37	4.25	9.85	4.19	.764	.717	—0.4	4.6	0.4	0.2	11:28	120
7 " 32 "	215.9	85.6	32.5	14.4	9.52	4.37	11.23	4.25	.858	.707	+0.4	3.5	1.4	0.4	2:53 p.m.	120
10 " 59 "	221.7	85.1	38.9	14.5	11.12	4.42	14.56	4.43	.952	.729	+1.6	3.6	1.7	0.4	6:20	120
14 " 34 "	225.5	85.9	35.0	16.3	10.00	5.34	13.39	5.40	.974	.809	+1.2	10.6	0.1	0.4	9:55	120
26 " 56 "	229.9	89.6	36.0	19.0	10.22	5.68	13.67	5.95	.971	.763	+1.0	6.6	0.1	0.4	10:13 a.m.	120

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[1] Although only one time is given, the litter and mother were run separately, there being not over 5 minutes difference in the time of starting the records. Both litter and mother records were of the same duration.

[2] Ration same as that given in Table 1 for rat 1032.

[3] "Milk Yield" was gauged by gain in body weight during a suckling period of 45 minutes.

*First 3 records there were 6 young, the remainder has 5 young except the last one which only had 4.