MAY, 1943 RESEARCH BULLETIN 368

UNIVERSITY OF MISSOURI COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION

M. F. MILLER, *Director*

Growth and Development

With Special Reference to Domestic Animals

LVIII. Resting Energy Metabolism and Pulmonary Ventilation in Growing Horses

SAMUEL BRODY, H. H. KIBLER, AND E. A. TROWBRIDGE

(Publication Authorized May 14, 1943)

Animal Husbandry Department and Dairy Department, Missouri Agricultural Experiment Station and the Bureau of Animal Industry, Agricultural Research Administration, United States Department of Agriculture, Cooperating

COLUMBIA, MISSOURI

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, and 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.

M. F. MILLER
Director Agricultural Experiment Station

ABSTRACT

Data are presented in numerical and graphic form, with critical discussion, for the resting energy metabolism (oxygen consumption and equivalent values in Calories and TDN during rest, standing and lying, but not in post absorptive condition) and pulmonary ventilation in relation to body weight in growing Percheron horses (females and geldings) and Shetland ponies. The results are compared critically with similar data on cattle. The results should be of interest to students of energy metabolism, physiology, nutrition, and growth, and to ventilating engineers.

Growth and Development

With Special Reference to Domestic Animals

LVIII. Resting Energy Metabolism and Pulmonary Ventilation in Growing Horses

SAMUEL BRODY, H. H. KIBLER, AND E. A. TROWBRIDGE

I. THE PROBLEM

One of the intriguing observations in animal nutrition is that the resting maintenance cost, or the so-called basal metabolism of mature animals of different size, does not vary with simple body weight but with a fractional power of body weight. Thus the basal metabolism of a 1000-pound mature animal is not 10-fold but 6 to 7-fold that of a 100-pound mature animal.[1] Many theories have been advanced[2] in explanation of this relation between resting metabolism and body weight in approximately mature animals of the same and of different species.

This report is concerned not with *mature* animals of *different species*,[1] but with the *same growing animals*, the same individuals. How do age and growth rate influence the resting maintenance cost?

In addition to data on resting maintenance cost of growing animals, basic for a science of animal nutrition and of considerable interest to the animal feeder, this bulletin also presents data on pulmonary ventilation rate (air volume exhaled or inhaled per unit time), oxygen consumption and, inferentially, carbon dioxide production and water-vapor exhalation,[3] which are basic for ventilating and air-conditioning engineering.

To broaden the generality of the conclusions based on our horse-metabolism data, a comparative analysis is presented on similar cattle-metabolism data.

[1]Missouri Agr. Exp. Sta. Res. Bul. 220.
[2]Missouri Agr. Exp. Sta. Res. Bul. 328.
[3]While there is some difficulty in computing precisely the water vaporization from air exhalation, it can be estimated closely. The literature indicates that at the point of exhalation the air is 2° to 3° C. below that of the mouth, and about 90% saturated with respect to this exhalation temperature. In man, the usual oral temperature is assumed to be 37° C. the air at expiration 34° to 36° C. and the water content of the expired air is about 80% of that of saturated air at 37° C., containing 0.032 to 0.037 gm. H_2O per liter expired air. For the literature see Newburgh, L. H., and Johnston, M. W., Physiol. Rev. 22, 1, 1942.

II. DATA. METHODS

The data on oxygen consumption and ventilation rates were obtained on six Percheron horses and two Shetland ponies (Table 1). The animals were usually measured before the morning feeding. The feeding, care, and management were the same as for the other animals in the horse barn. They were possibly more gentle because they were trained for the measurements and more used to being handled.

TABLE 1.—EXPERIMENTAL ANIMALS.

No.	Metabolism-Measurement Period, Months	Birth Month	Age Bred Months
	Percherons, *Females*		
15	Birth to 63rd	March	36
18	Birth to 58th	April	36
20	Birth to 58th	May	35
	Percherons, *Geldings*		
16	Birth to 59th	March	
17	Birth to 58th	April	
19	Birth to 61st	April	
	Ponies, *Females*		
IV	Birth to 39th	March	
V	2nd to 13th	May	

The method of measuring the metabolism was previously described.[4] The rate of oxygen consumption is measured directly by the rate of decline of the oxygen bell, recorded automatically on a clock kymograph.

The ventilation rate, that is the inhaled or exhaled air volume per minute, is computed from the amplitudes of the up-and-down movements of the oxygen bell corresponding to the inspiratory and expiratory movements of the lungs as recorded on the clock kymograph.

As the animals were usually measured before the morning feeding, 8 to 12 hours after the preceding evening feeding, they were not in post-absorptive condition since, unlike humans, horses do not reach post-absorptive condition in 12 hours, but in, perhaps, 48 hours (more or less depending on age and other factors). The oxygen-consumption data thus represent not "basal metabolism" but normal morning metabolism at rest in standing and occasionally lying position. It will be presently shown that the metabolism in horses is not higher, and perhaps lower, during standing than during lying. Consequently, most of the measurements were made in the standing position. The data thus represent approximately the minimum normal (not fasting)

[4]Missouri Agr. Exp. Sta. Res. Bul. 143, pp. 6 to 15.

maintenance cost. Table 2 presents these data in terms of different units, computed from the equations in the text.

The shape and slope of the curve relating metabolism to body weight vary from animal to animal depending on the date of birth, seasonal and other factors affecting growth and metabolism. Differences in intestinal "fill" with the associated heat increment of feeding (while the animals were regularly fed the preceding evening, they usually also had access to some hay or pasture at night) also contributed to the variability of the data. In brief, the data represent oxygen consumption not of laboratory animals living under a calorimeter-chamber regime, but of animals living and cared for under typical farm practice and measured under conditions representative of normal rest.

III. GENERALIZATIONS

Large bodies of numerical data are not necessarily useful but are often confusing unless welded together into a simple generalization, a so-called "law" in the form of an equation, which may be used for practical prediction purposes.

The simplest and best known generalization previously used for relating metabolism to body weight in *mature* animals of *different species*[1] *is* the relative-growth equation.[2]

$$Y = aX^{b} \qquad (1)$$

in which Y is metabolism at body weight X. We shall also employ it for generalizing the relation of pulmonary ventilation and oxygen consumption to body weight in *growing* animals within the *same species*, horses.

1. **Relation of Pulmonary Ventilation to Body Weight in Growing Horses.**—Equation (1) was fitted (by the method of least squares) to the data on the minute volume of pulmonary ventilation—that is to the volume of air exhaled or inhaled per minute (at S.T.P.)—with the result shown in Fig. 1. The slope of the curve, that is the value of the exponent b in equation (1), is 0.68, meaning that at any point on the curve the ventilation rate is increasing only 0.68 as rapidly as body weight.

It may be recalled that the slope of the curve, that is the value of the exponent b of equation (1), relating basal metabolism, Y, to body weight, X, of *mature* animals of *different species* is[1] 0.73, not so very different, yet definitely higher than the value of 0.68 given in Fig. 1 for the pulmonary ventilation of the *same growing* horses. This is, philosophically, an interesting observation, especially since the ventilation and metabolic rates tend to parallel each other, to be directly proportional to each other.

TABLE 2A.—PREDICTION TABLE FOR RESTING ENERGY MAINTENANCE COST AND VENTILATION RATE IN GROWING PERCHERON HORSES (FEMALES).
(Computed from Equations in Figs. 1 and 2.)

Body Weight		Approximate age	Energy Maintenance Cost per 24 hrs.						Oxygen Consumption (S.T.P.) Per 24 hours				Ventilation Rate (S.T.P.) Per minute				Per day	Ratio of oxygen consumption to ventilation rate
			Calories			B.T.U.		Equivalent in TDN Lbs.[3]	Liters		Cu. ft.		Liters		Cu. ft.		Liters	% O₂ consumed / Air inhaled
Kgs.	Lbs.	Mos.	Total[1]	Per Kg.	Per Sq. M.[2]	Total	Per Lb.		Total	Per Kg.	Total	Per Lb.	Total	Per Kg.	Total	Per Lb.	Per Sq. M.	
75	165.3	.1	3850	51.3	2540	15280	92	2.1	800	10.6	28.2	.171	28.7	.383	1.01	.0061	27220	1.93
100	220.5	.7	4497	45.0	2470	17840	81	2.5	930	9.3	32.9	.149	33.7	.337	1.19	.0054	26660	1.92
125	275.6	1.3	5073	40.6	2420	20130	73	2.8	1050	8.4	37.1	.135	39.2	.314	1.38	.0050	26940	1.86
150	330.7	1.8	5598	37.3	2380	22210	67	3.1	1160	7.7	41.0	.124	44.4	.296	1.57	.0047	27210	1.81
175	385.8	2.4	6083	34.8	2350	24140	63	3.4	1260	7.2	44.5	.115	49.3	.282	1.74	.0045	27410	1.78
200	440.9	2.9	6538	32.7	2320	25940	59	3.6	1360	6.8	47.8	.108	54.0	.270	1.91	.0043	27610	1.74
225	496.0	3.4	6968	31.0	2300	27650	56	3.8	1440	6.4	51.0	.103	58.5	.260	2.07	.0042	27770	1.71
250	551.1	4.0	7375	29.5	2280	29260	53	4.1	1530	6.1	54.0	.098	62.9	.252	2.22	.0040	27960	1.69
275	606.3	4.8	7765	28.2	2260	30810	51	4.3	1610	5.8	56.8	.094	67.1	.244	2.37	.0039	28080	1.67
300	661.4	6.0	8138	27.1	2240	32290	49	4.5	1690	5.6	59.6	.090	71.2	.237	2.51	.0038	28200	1.65
350	771.6	8.5	8845	25.3	2210	35100	46	4.9	1830	5.2	64.7	.084	79.0	.226	2.79	.0036	28400	1.61
400	881.8	14.0	9507	23.8	2180	37720	43	5.2	1970	4.9	69.6	.079	86.5	.216	3.05	.0035	28580	1.58
450	992.1	18.1	10130	22.5	2150	40200	40	5.6	2100	4.7	74.1	.075	93.8	.208	3.31	.0033	28780	1.55
500	1102	23.0	12450	24.9	2480	49400	45	6.9	2580	5.2	91.1	.083	100.7	.201	3.56	.0032	28910	1.78
550	1212	26.0	13655	24.8	2560	54180	45	7.5	2830	5.1	100.0	.082	107.5	.195	3.80	.0031	29060	1.83
600	1323	29.0	14858	24.8	2640	58960	45	8.2	3080	5.1	108.7	.082	114.0	.190	4.03	.0030	29180	1.88
650	1433	33.0	16055	24.7	2710	63710	44	8.8	3330	5.1	117.5	.082	120.4	.185	4.25	.0030	29300	1.92
700	1543	40.0	17252	24.6	2780	68460	44	9.5	3580	5.1	126.3	.082	126.6	.181	4.47	.0029	29400	1.96
750	1654	49.0	18448	24.6	2850	73200	44	10.2	3820	5.1	135.0	.082	132.7	.177	4.69	.0028	29510	2.00
800	1764	60.0	19638	24.5	2910	77920	44	10.8	4070	5.1	143.7	.081	138.6	.173	4.89	.0028	29590	2.04

[1]The heat production was computed on the assumption that one liter of oxygen has a heat equivalent of 4.825 Calories.

[2]Surface area was computed from the equation, surface area in sq. meters = 0.1 (weight in kg.)$^{0.63}$. See Missouri Agr. Exp. Sta. Res. Bul. 115, p. 30.

[3]Computed on the assumption that one lb. TDN (total digestible nutrients) is equivalent to 1814 Cal. or 1 gm. of TDN to 4 Cal.

TABLE 2B.—PREDICTION TABLE FOR RESTING ENERGY MAINTENANCE COST AND VENTILATION RATE IN GROWING PERCHERON HORSES (GELDINGS).
(Computed from Equations in Figs. 1 and 2.)

Body Weight		Approximate age	Energy Maintenance Cost per 24 hrs.						Oxygen Consumption (S.T.P.)				Ventilation Rate (S.T.P.)					Ratio of oxygen consumption to ventilation rate
			Calories			B.T.U.		Equivalent in	Per 24 hours				Per minute				Per day	
									Liters		Cu. ft.		Liters		Cu. ft.		Liters	%
Kgs.	Lbs.	Mos.	Total[1]	Per Kg.	Per Sq. M.[2]	Total	Per Lb.	TDN Lbs.[3]	Total	Per Kg.	Total	Per Lb.	Total	Per Kg.	Total	Per Lb.	Per Sq. M.	O_2 consumed / Air inhaled
75	165.3	.1	3861	51.5	2540	15320	93	2.1	800	10.7	28.2	.171	28.7	.383	1.01	.0061	27220	1.94
100	220.5	.6	4484	44.8	2460	17790	81	2.5	930	9.3	32.8	.149	33.7	.337	1.19	.0054	26660	1.91
125	275.6	1.0	5036	40.3	2410	19980	72	2.8	1040	8.4	36.9	.134	39.2	.314	1.38	.0050	26940	1.85
150	330.7	1.6	5537	36.9	2360	21970	66	3.1	1150	7.6	40.5	.122	44.4	.296	1.57	.0047	27210	1.80
175	385.8	2.2	5981	34.2	2310	23730	62	3.3	1240	7.1	43.8	.114	49.3	.282	1.74	.0045	27410	1.75
200	440.9	2.8	6430	32.2	2280	25510	58	3.5	1330	6.7	47.1	.107	54.0	.270	1.91	.0043	27610	1.71
225	496.0	3.4	6837	30.4	2250	27130	55	3.8	1420	6.3	50.0	.101	58.5	.260	2.07	.0042	27770	1.68
250	551.1	4.0	7221	28.9	2230	28650	52	4.0	1500	6.0	52.8	.096	62.9	.252	2.22	.0040	27960	1.65
275	606.3	4.8	7588	27.6	2200	30110	50	4.2	1570	5.7	55.6	.092	67.1	.244	2.37	.0039	28080	1.63
300	661.4	6.0	7939	26.5	2180	31500	48	4.4	1640	5.5	58.1	.088	71.2	.237	2.51	.0038	28200	1.60
350	771.6	9.5	8602	24.6	2150	34130	44	4.7	1780	5.0	62.2	.081	79.0	.226	2.79	.0036	28400	1.56
400	881.8	14.0	9221	23.0	2120	36590	42	5.1	1910	4.8	67.5	.076	86.5	.216	3.05	.0035	28580	1.53
450	992.1	18.0	9803	21.8	2090	38900	40	5.4	2030	4.5	71.8	.072	93.8	.208	3.31	.0033	28780	1.50
500	1102	24.0	12029	24.1	2400	47730	43	6.6	2490	5.0	88.0	.080	100.7	.201	3.56	.0032	28910	1.72
550	1212	27.3	13461	24.5	2530	53410	44	7.4	2790	5.1	98.5	.081	107.5	.195	3.80	.0031	29060	1.80
600	1323	35.0	14917	24.9	2650	59190	45	8.2	3090	5.2	109.2	.083	114.0	.190	4.03	.0030	29180	1.88
650	1433	50.0	17892	25.2	2770	65040	45	9.0	3400	5.2	120.0	.084	120.4	.185	4.25	.0030	29300	1.96
700	1543	58.0	17890	25.6	2880	70990	46	9.9	3710	5.3	130.9	.085	126.6	.181	4.47	.0029	29400	2.03
750[4]	1654	...	19410	25.9	3000	77020	47	10.7	4020	5.4	142.1	.086	132.7	.177	4.69	.0028	29510	2.11
800[4]	1764	...	20944	26.2	3100	83110	47	11.5	4340	5.4	153.3	.087	138.6	.173	4.89	.0028	29590	2.17

[1]The heat production was computed on the assumption that one liter of oxygen has a heat equivalent of 4.825 Calories.

[2]Surface area was computed from the equation, surface area in sq. meters = 0.1 (weight in kg.)$^{.63}$. See Missouri Agr. Exp. Sta. Res. Bul. 115, p. 30.

[3]Computed on the assumption that one lb. TDN (total digestible nutrients) is equivalent to 1814 Cal. or 1 gm. of TDN to 4 Cal.

[4]Computations for these body weights are extrapolations beyond the range of actual data.

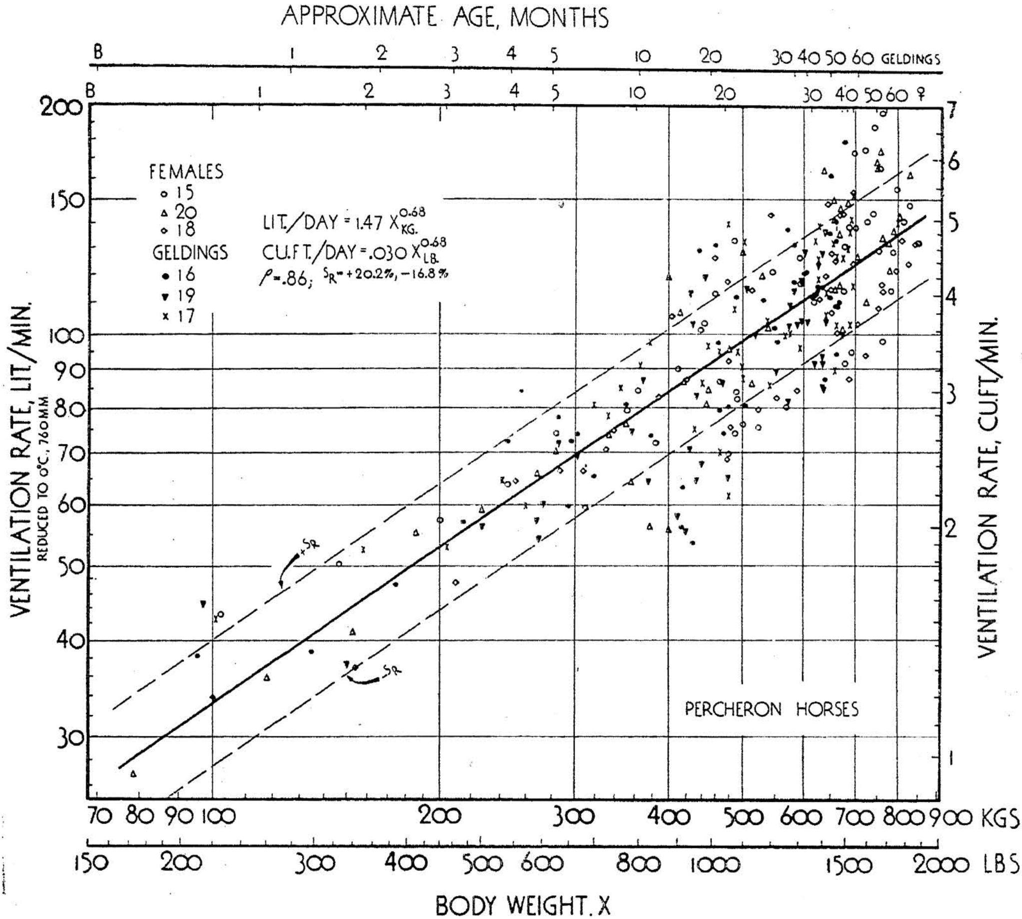

Fig. 1.—Minute volume of pulmonary ventilation (air volume per minute exhaled or inhaled) plotted against body weight on a logarthmic grid. The heavy line reprsents the given equation, the dash line the standard error of estimate.

The scatter of the data points about the mean curve is not very satisfactory. The value of the standard error of estimate, S_R, is high, +20% and —17%, meaning that 2/3 of the data points are included within these values, represented by broken curves in Fig. 1, within +20% and —17% of the average line. These high values of the standard error may be attributed, in part, to the fact that unlike in man, the resting pulmonary ventilation rate in horses is also used for body-temperature regulation, for regulating the rate of water vaporization from the respiratory and oral systems, and so varies with environmental temperature and season.

2. **Relation of Resting Metabolism (Oxygen Consumption) to Body Weight in Growing Horses.**—Figs. 2 and 3 represent the resting metabolism (oxygen consumption, heat production, TDN consumption for maintenance alone) in relation to body weight. Approximate ages are indicated on the upper axis.

The pony data, in Fig. 2, are distributed approximately linearly, and the slope b in equation (1) is about 0.55; meaning that the (differential) increase in metabolism is a little over one-half as rapid as the increase in body weight during growth; increasing body weight 100% increases the resting maintenance cost not 100%, but only 50%.

The pony data cover a little over 2 years. The Percheron data, in Fig. 2b, go on to a much later age, to about 5 years, and the distribution of the data following about 2 years appears more complex. There appears to be a "break" in the curve at body weight 500 Kg. (1100 lb.). The slope, the value of the exponent b in equation (1), is the same as for the pony up to the "break," followed by a much steeper, almost doubled, slope. Preceding the break the slope is about 0.5; following, it is about 1.0. The absolute values and the slopes appear to be higher for the females than the geldings.

The significance of the break in the curve and the sudden rise in steepness of slope is not clear. However, the break coincides with the time when the animals mature rapidly and begin to work, and we have previously demonstrated[5] that the metabolism of mature horses varies not with surface area or with $W^{.73}$ but directly with body weight, with $W^{1.0}$.

3. **The Relation Between Standing and Lying Oxygen Consumption.**—The extra energy cost of standing above lying is about 9% in men,[6] cattle and sheep.[7] Fig. 2 shows that in horses, on the contrary, the rate of oxygen consumption (metabolism) is the same

[5]Kibler, H. H., and Brody, S., Missouri Agr. Exp. Sta. Res. Bul. 367, 1943
[6]Benedict, F. G., and Johnson, A., Am. Phil. Soc. 58, 89, 1919.
[7]Hall, W. C., and Brody, S., Missouri Agr. Exp. Sta. Res. Bul. 180, 1933.

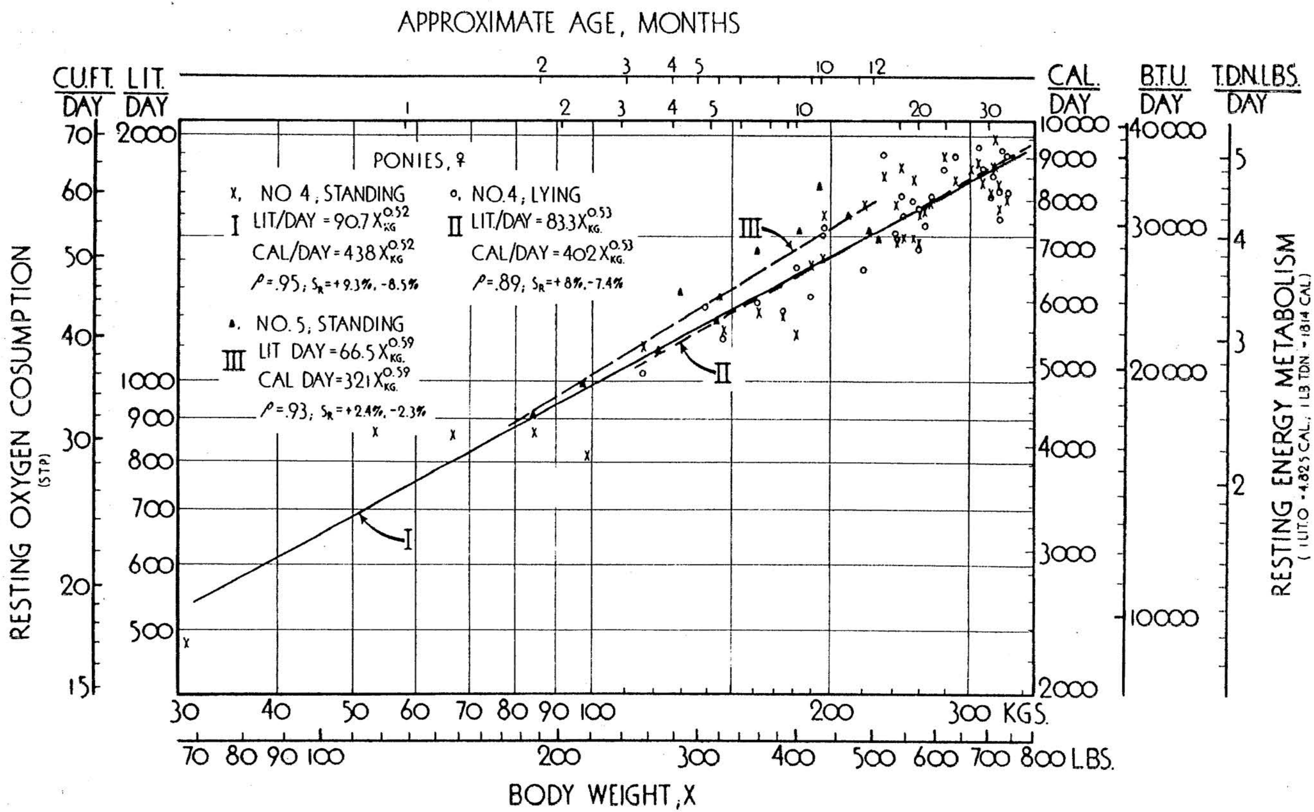

Fig. 2.—Resting oxygen consumption (left axis) and heat production in terms of Cal/day, B.t.u./day, and TDN lb./day (right axis) plotted against body weight for standing (curve I) and lying (curve II) pony.

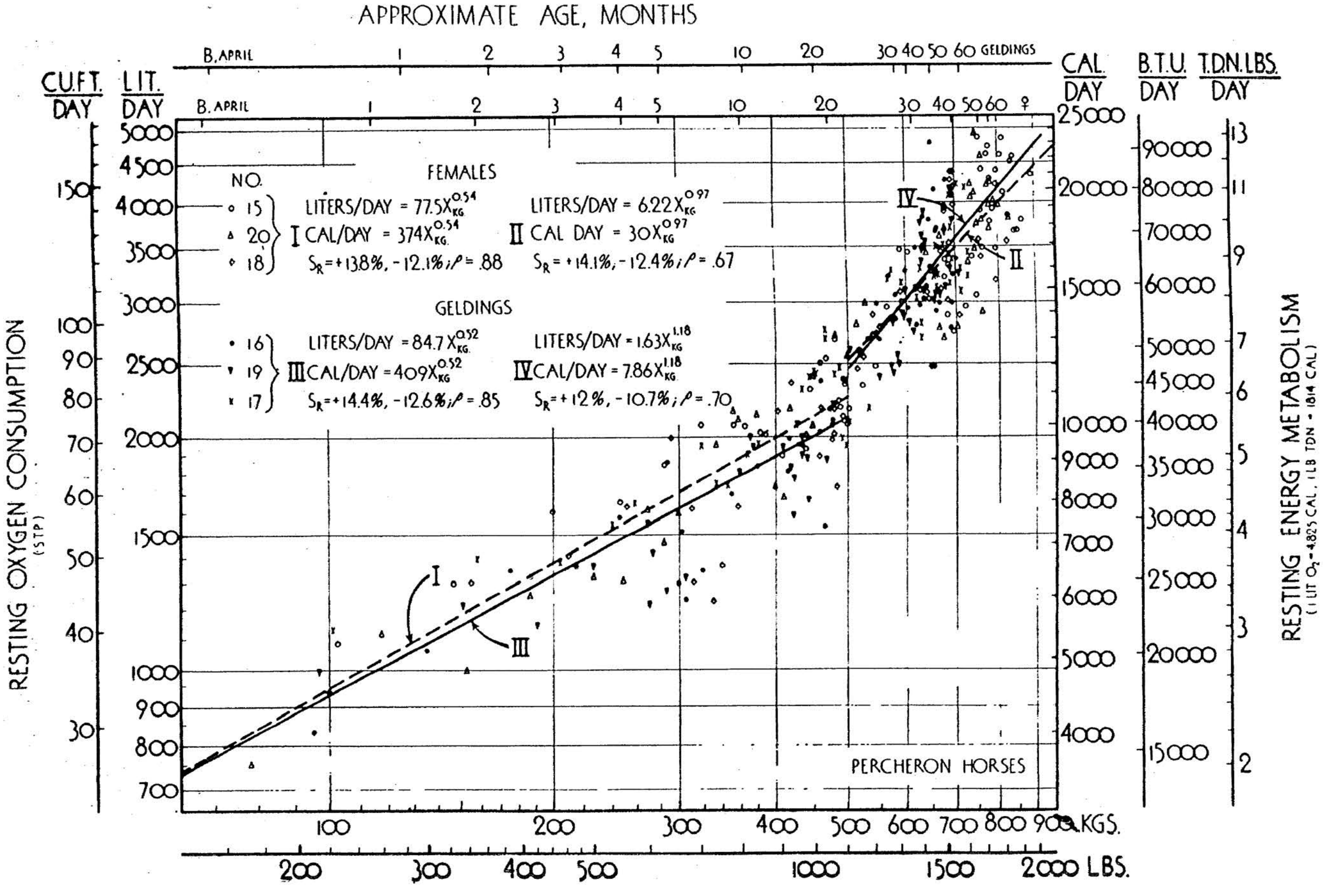

Fig. 3.—Same as Fig. 2 but for Percheron horses, females and geldings.

during standing and lying during the entire period of growth. A year or two later, when the two ponies represented in Fig. 2 became quite mature, Winchester[8] measured their oxygen consumption during lying and standing and found no difference, indeed slightly higher metabolism during lying than standing (404 Cal/hr. during standing and 432 during lying; 407 Cal./hr. standing and 448 lying). This peculiarity of horses is probably associated with their unusually powerful suspensory and check ligaments. This may explain why horses prefer to sleep while standing while other farm animals prefer to sleep while lying. It is useful to know that it is not necessary to have horses in the lying position to measure their "basal metabolism." The standing position yields minimal metabolic values in this species. This is fortunate because it is rather difficult to get a horse to lie down quietly.

4. **Comparative Summary.**—The numerical data summarized in Table 2 are self-explanatory and reasonable with one exception, namely the much higher ventilation rate in relation to oxygen consumption in horses, and also in cattle,[9] than in man. This is shown in the last column of the table, the low $\frac{O_2 \text{ consumed}}{\text{air inhaled}}$ ratios. The use of the closed-circuit metabolism apparatus may have contributed, but only in part, to the high ventilation rate. Carpenter[10] reported an average pulmonary ventilation value for man of 6.32 lit/min. for closed-circuit apparatus and 5.38 lit/min. for open-circuit apparatus. Another explanation for our relatively high pulmonary ventilation rates was offered by Carpenter,[11] namely that in comparison to man, cattle and horses sweat but slightly; and since all the warm-blooded species investigated appear to dissipate approximately the same percentage of their heat production by water vaporization, it follows that the relatively slightly-sweating horses and cows should have a correspondingly higher pulmonary-ventilation rate so as to facilitate a correspondingly higher vaporization rate from the pulmonary-oral surfaces and thus compensate for the lower vaporization loss from the skin.

Another possibility is that the larger the animal the higher the ventilation rate in comparison to oxygen consumption. This, too, is related to body-temperature regulation. We hope to present the evidence for this idea in a future report.

It is interesting to compare the metabolism of growing horses with that of cattle, previously reported.[9] This is shown in Fig. 4. The upper

[8]Winchester, C. F., Science, 97, 24, 1943.
[9]Brody, S., Kibler, H. H., and Ragsdale, A. C., Missouri Agr. Exp. Sta. Res. Buls. 335, 1941, and 350, 1942.
[10]Carpenter, T. M., Boston Med. and Surg. J. 181, 334, 368, and 285, 1919.
[11]Carpenter, T. M., Letter to S. B., Feb. 4, 1943.

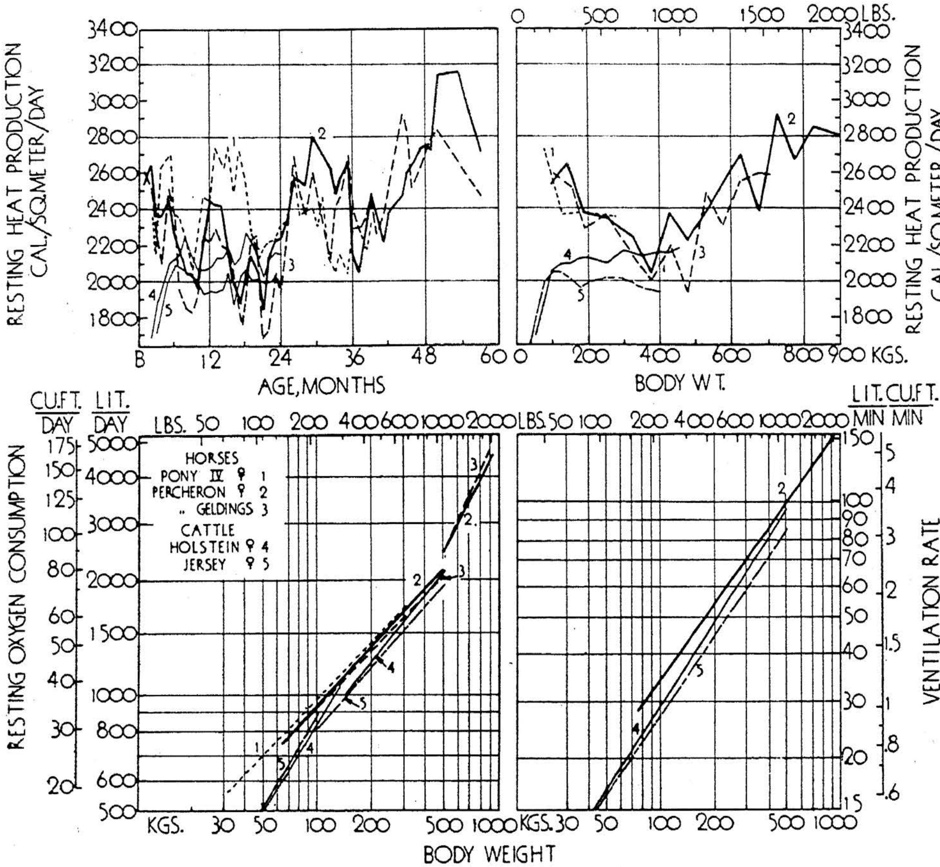

Fig. 4—Comparison of horse and cattle data for given ages and body weights in terms of Cal/sq. m/day and total metabolism as function of body weight.

left curves represent metabolism per unit area as function of age. The striking difference is that the cattle curves, 4 and 5, rise steeply with increasing age up to 6 months; the horse curves, 1 and 2, decline. The early high level and decline of the horse curves (as contrasted to the rise in the cattle curves) is as artifact. The calves acquiesced to the metabolism measurements from the outset; the colts did not; they were rebellious and not really relaxed. It took them several months to acquiesce fully. The upper right curves represent metabolism per unit surface area as function of body weight. Here again, the cattle curves, 4 and 5, rise steeply until body weight 100 Kg. (220 lbs.), then remain horizontal; the horse curves, 1 and 2, on the other hand, decline until over 300 Kg. (700 lb.) then rise. The lowest metabolism per unit area in horses is about 2000 Cal/sq. meter/day, and it rises up to 2800 Cal/sq. meter/day at full maturity, while the resting metabolism of cattle never exceeds 2100-2200 Cal/sq. meter/day. The pulmonary ventilation level in cattle is below that in horses, but they parallel in slope.

Summarizing, the pulmonary ventilation rate in horses increases with, approximately, the 2/3 power of body weight as contrasted to that in cattle which increases with, approximately, 3/4 power of body weight; the resting oxygen consumption (minimum maintenance cost) during the first two years of postnatal growth in horses increases with, approximately, the 0.53 power of body weight as contrasted to that in cattle which increases with, approximately, the 0.60 power of body weight. While cattle have a 9% heat increment of standing, horses do not. There are other differences between horse and cattle curves discussed in the text. Prediction values are given for ventilation rates and energy metabolism in various units and their significance is discussed.