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M. F. MILLER, *Director*

Growth and Development

With Special Reference to Domestic Animals

LVII. An Index of Muscular-Work Capacity

H. H. KIBLER AND SAMUEL BRODY

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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

Oxygen consumption rate in small and large work horses (at 16° to 25° C.) duing rest and work on a horizontal treadmill was related to pulse rate and body weight, and measures of cardio-respiratory capacity were computed. Among the more important findings (illustrated by charts and tables) were the following: Oxygen consumption is directly proportional to body weight in nearly mature work horses of different size. Oxygen pulse (oxygen consumption per minute divided by pulse rate per minute) tends to be directly proportional to body weight in mature animals of different species. Oxygen pulse per kilogram of body weight tends to be constant for all body weights (Table 2) but appears to vary with training and muscular-work capacity; oxygen pulse per kilogram of body weight may thus be taken as an index of work capacity, an objective rating scale for comparing work capacity in horses and mature animals of other species. When oxygen pulse per kilogram of body weight is high during rest and shows a normal rise during work, work capacity is assumed to be high; when this index is low during rest and work, work capacity is assumed to be low. The index values found for horses were compared to index values computed for athletes and sedentary men.

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External appearance—size and proportions—does not always distinguish the champion from a competitor, the superior from the average. Important factors are hidden and are often disclosed only by special tests. The work capacity of the automobile, for example, is correlated with the power of the engine and that of the horse or man with the oxygen-transport capacity of the heart and related cardiorespiratory organs which supply oxygen to the working muscles.

Oxygen-transport capacity is related to several factors among which is pulse rate. It is generally known that great athletes have a slower pulse rate than non-athletes, and that when other conditions are equal, the physically fit have a lower pulse rate than the physically unfit. Since the rate of oxygen consumption[1] is probably the same in slow-pulse and rapid-pulse individuals, it follows that high oxygen-transport capacity is associated with high oxygen consumption per heart beat or per pulse. This oxygen intake per pulse, cc. of oxygen consumed per pulse of the heart, is called *oxygen pulse,* a basic concept which we shall use throughout this report.

The magnitude of the oxygen pulse is dependent on the size of the heart and the size of the animal; it is over 100,000 times greater in the elephant than in the mouse. Oxygen pulse, therefore, cannot be used as an index of equivalent work capacity in animals of different size. To estimate physiologically equivalent work capacity in animals of different size, we shall develop and employ the work capacity index, *oxygen pulse per kilogram of body weight,* and the major purpose of this bulletin is to report the results with special reference to work horses.

[1]From the energetic viewpoint, hard muscular work is a rapid transformation of potential energy of body fuel, mostly glucose, into work.

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O + 680 \text{ Cal.}$$

glucose 134.4 l.
(180 g.) (6 x 24.4)

For each mol., or 180 g. of glucose, 134.4 liters of O_2 are consumed, generating in this process about 680 Cal. of energy, or 680/134.4, about 5 Cal. per liter of O_2 consumed. Of this energy up to 25% may be converted into useful work. We measured the bodily energy expended during work by the rate of oxygen consumption.

Few tests of physical ability have been applied to horses[2] in comparison to the numerous tests devised and employed in measuring the physical capacity of man.[3] Experimental work on horses is expensive and time consuming. Many of the tests applied to human subjects require greater cooperation than can be obtained from animals.

Tests which indicate work capacity are especially needed, however, in measuring trends in breeding programs in horses. There is a need for developing an index of work capacity in horses, an objective rating scale comparable to measures of milk production in dairy cattle and egg production in poultry. The oxygen pulse per kilogram of body weight appears to be such an objective index of muscular work capacity in horses and other species. The special value of this index lies in its usefulness in comparing subjects of different body size and in the basic nature of the function it measures.

[2]The energetic efficiency of work in horses at various work levels was reported by: R. C. Proctor, S. Brody, M. M. Jones, and D. W. Chittenden, Missouri Agr. Exp. Sta. Research Bulletin 209, 1934; by S. Brody and Richard Cunningham, Id., Res Bul. 244, 1936; and by S. Brody and E. A. Trowbridge, Id., Res. Bul. 383, 1937. Tests of performance in saddle horses and other light horses were made by R. W. Phillips, G. W. Brier, and W. V. Lambert, Pub. Animal Husbandry Division, Bureau Animal Industry, Washington, D. C., 1940. Dynamometer tests were discussed by R. W. Phillips, M. A. Madsen, and H. H. Smith, Utah State Agr. Exp. Sta. Circular 114, 1940. The training and testing program at the U. S. Morgan Horse Farm was reported by R. W. Phillips, S. R. Speelman, and J. O. Williams, Vermont Horse and Bridle Trail Bulletin, Jan. 1942.

[3]Many of the tests on man were discussed by J. H. McCurdy and L. A. Larson, The Physiology of Exercise, Lea & Febiger, Philadelphia, 1939.

DATA AND THEIR ANALYSES

The method of securing our data on horses is illustrated in Fig. 1. For purposes of generalization, we are supplementing these data on horses with data on other species taken from the literature.

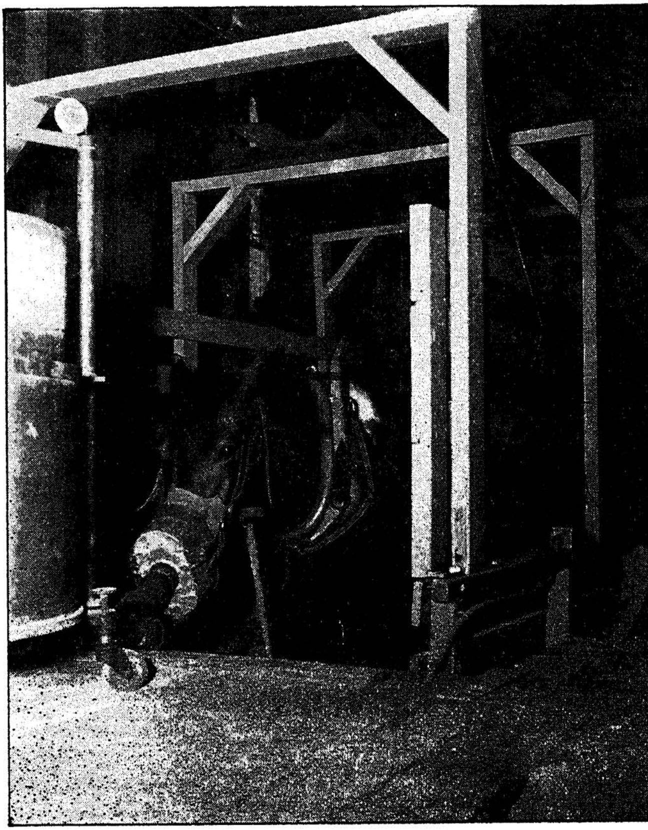

Fig. 1.—Photograph of treadmill and metabolism apparatus (described in Mo. Agr. Exp. Sta. Res. Bul. 209 and 244).

Our data for average oxygen consumption and pulse rate for horses standing at rest are given in Table 1. The corresponding individual measurements taken while the horses were working on the treadmill are too numerous to tabulate, but are plotted in Fig. 2. These data are restricted to measurements made at room temperatures, between 16° and 25° C., as environmental temperature is known[4] to have a pronounced effect on heart rate during physical work.

4Dill, D. B., Edwards, H. T., Bauer, P. S., & Levenson, E. J., Arbeitsphysiol. 4, 508, 1931.

TABLE 1.—OXYGEN CONSUMPTION AND PULSE RATE OF HORSES, STANDING*

Animal No.	Observations	Breed	Sex	Age years	Live weight kg.	Live weight lb.	Oxygen consumption cc./min.	Oxygen consumption cu. in./min.	Pulse rate	Barn Temp. °C.
A. Averages for May and June records only.** (Plotted in Fig. 6)										
2	7	Shetland pony	Female	5½	290	639	915	56	44	26.0
3	4	Shetland pony	Gelding	3½	331	730	1143	70	41	23.8
4	5	Shetland pony	Female	2¼	288	635	1171	71	53	22.8
15	11	Percheron	Female	3	685	1510	2307	141	46	23.0
16	18	Percheron	Gelding	3	574	1265	2176	133	43	21.8
17	4	Percheron	Gelding	4	689	1519	2542	155	39	23.3
18	9	Percheron	Female	3	663	1462	2269	138	45	24.1
19	3	Percheron	Gelding	4	632	1393	2318	141	39	25.7
20	7	Percheron	Female	2¼	536	1182	2138	130	49	23.9
B. Averages, standing, taken between treadmill work periods at 1.15 mi/hr., room temperature range 16° C. to 25° C.										
2	4	Shetland pony	Female	4¼	265	584	857		41.0	21.0
3	3	Shetland pony	Gelding	2	274	603	908		40.7	17.0
19	7	Percheron	Gelding	4½	684	1509	2262		39.3	19.2
C. Averages, standing, taken between treadmill work periods at 2.2 mi/hr., room temperature range 16° C. to 25° C.										
2	21	Shetland pony	Female	4¼	273	601	908		38.7	17.0
3	10	Shetland pony	Gelding	2	265	584	898		41.9	17.0
19	16	Percheron	Gelding	4½	709	1563	2159		42.0	20.0

*Oxygen consumption and pulse rate in horses appear to be no higher for standing than for lying. Winchester, C. F., Science 97, 24, 1943; Brody, S., Kibler, H. H., & Trowbridge, E. A., Missouri Agr. Exp. Sta. Res. Bul. 367, 1943.

**The data were restricted to a limited but definite period of the year to eliminate seasonal variation and to lessen the range of temperature variations.

Some data from the literature are included in Table 2 and Figs. 4 and 7.

The rate of O_2 consumption is taken to be the product of three *work capacity reserves*: stroke volume of the heart or systolic output, arterio-venous difference in O_2 content of the blood, and pulse rate. The relation between these various factors may be expressed in the equation form:

$$O_2 = vdf \qquad (1)$$

The units of measurement usually employed are:

O_2, oxygen consumption, cc/min.

v, stroke volume, liters of blood per systole

d, arterio-venous difference in O_2 content of blood, cc/liter

f, pulse rate or frequency per minute

During mild exercise, the relation between pulse rate, f, and O_2 consumption rate, O_2, may be quite variable because of the changing number and caliber of open capillaries in the muscles concerned and because also of the increased venous return of blood to the heart by the pumping action of the muscles. These effects, discussed by Krogh[5] and Grollman[6] may result in greater change in the stroke volume, v,

5Krogh, A., The anatomy and physiology of capillaries, Revised Edition. New Haven, 1929; Comparative physiology of respiratory mechanisms, Univ. of Penn. Press, Philadelphia, 1941.

6Grollman, A., Am. J. Physiol. 96, 8, 1931.

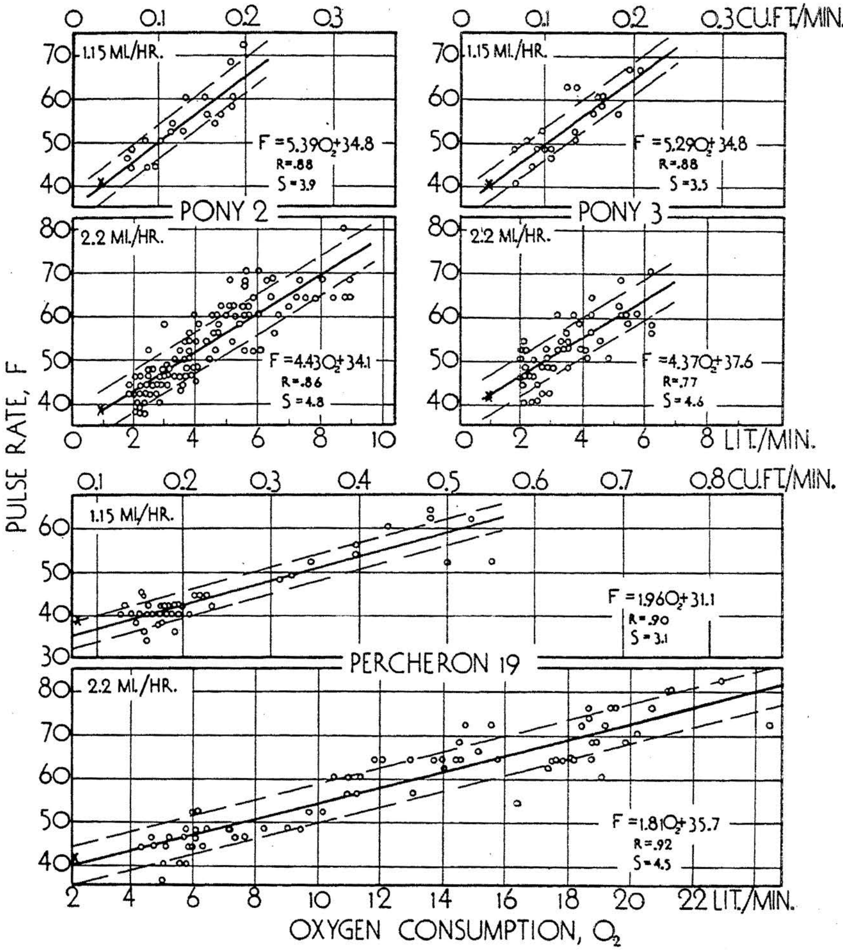

Fig. 2.—Pulse rate as a function of total oxygen consumption during rest and work on a treadmill at two different speeds. Linear equations (heavy solid lines) were fitted to the individual measurements by the method of least squares. The standard error of estimate, S (light broken lines) and the coefficient of correlation, r, are given in each case. Individual measurements are shown as open circles and average standing values as X's.

or arterio-venous difference, d, than in pulse rate, f. Smith[7] noted a decrease in pulse rate in slow walking over standing in several human subjects, although the oxygen consumption rate was doubled. Hall and Brody[8] reported that in human subjects and horses walking at 1.15 mi/hr., the pulse rates were 0 to 8 per cent higher than for standing, the metabolism showing increases of 64 to 119 per cent. They reported

[7]Smith, H. M., Carnegie Inst. Wash. Pub. No. 309, 1922.
[8]Hall, W. C., and Brody, S., Missouri Agr. Exp. Sta. Res. Bul. 208, p. 8, 9, 1934.

increases in pulse rate in cattle as high as 20 per cent for the same conditions.

Experimental evidence on man indicates[9,10,11] that within certain limits (from moderately mild exercise up to moderately heavy exercise) pulse rate is almost linearly related to oxygen consumption. The same appears to be true for horses. We have fitted linear equations to the data for horses working on the treadmill (Fig. 2), and it appears that for the given range there is no marked departure of the data from the fitted lines. These linear equations will accordingly be used as a convenient means of averaging the data for further calculations, without, however, implying that the relation between pulse rate and oxygen consumption is linear.

Factors other than the severity of exercise affect the relation between pulse rate and oxygen consumption in a given subject. Thus Fig. 2 shows that for a given increase in oxygen consumption, the pulse rate increases more slowly for the 2.2 than for the 1.15 mi/hr. work rates, probably indicating an increased systolic output at the higher speed. Our further analysis is confined to the 2.2 mi/hr. speed.

The effect of body size on the relation of pulse rate to oxygen consumption is shown in Fig. 3 where the equation lines of Fig. 2 (2.2 mi/hr.) are brought together on the same scale. To test the validity of our methods and results we show also in Fig. 3, equation lines we fitted to data by Bock et al.[9] for three men described as follows:

Subject	Physical condition	Age yrs.	Weight Kg.	Height cm.
De Mar	Marathon runner (in training)	39	61.5	163
C. V. C.	Sedentary (non-athletic)	25	59.0	163
D. B. D.	Sedentary (formerly athletic)	35	71.5	180

A comparison of the curves of Fig. 3 indicates that on an absolute basis and per liter of oxygen consumed, the pulse rate increases about ten times faster in the men than in the ponies, and about 2.5 times faster in the ponies than in the draft horses. These differences are, in the main, due to differences in body size and they indicate the need for a method of equalizing body size when comparing subjects of unlike size.

Equalization of oxygen consumption rate for body size may be made in the case of horses by dividing oxygen consumption rate during work either by body weight or by the oxygen consumption rate during rest (shown respectively by the horizontal axis, center section and the horizontal axis, lower section, Fig. 3). In man, on the other

[9]Bock, A. V., Vancaulaert, C., Dill, D. B., Folling, A., and Hurxthal, L. M., J. Physiol. 66, 136, 1928.
[10]Schneider, E. D., Am. J. Physiol. 97, 353, 1931.
[11]Taylor, Craig, Am. J. Physiol. 135, 27, 1941.

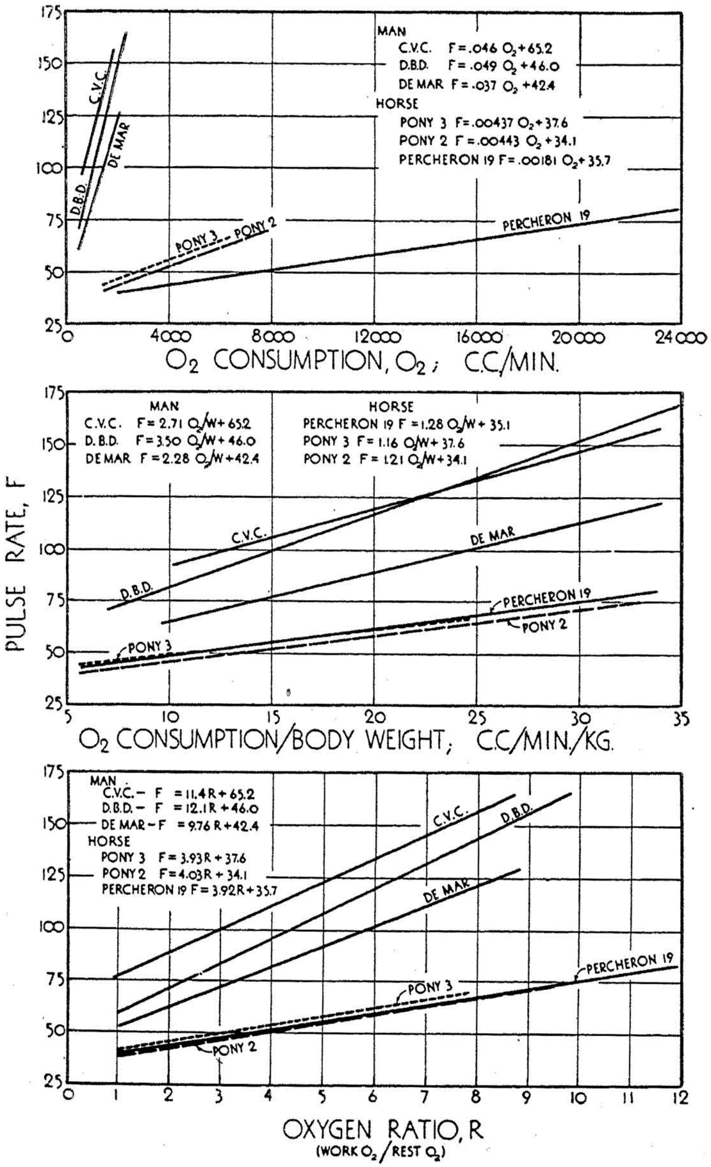

Fig. 3.—Pulse rate in horses working on a treadmill and in men working on a bicycle ergometer as a function of total oxygen consumption. The linear equations of Fig. 2 for horses (2.2 mi/hr.) are compared on the same absolute scales (upper section) with linear equations we fitted to data on man by Bock et al.[9] We used the 1927 data for De Mar. In the center section pulse rate is plotted against oxygen consumption per kilogram of body weight. In the lower section pulse rate is plotted against oxygen consumption during work divided by oxygen consumption during rest.

hand, it is known[12] that basal metabolism is not proportional to body weight; equalization for body size must, therefore, be made by the ratio method, by dividing the oxygen consumption rate during work by the oxygen consumption rate during rest. There is still a considerable difference in pulse rate between the men and the horses, some of which can be explained by differences in experimental techniques: the men breathed air while the horses breathed oxygen-rich mixtures; pulse rates were taken on the men presumably during work and on the horses immediately after stopping work. These factors, however, should not influence the data taken under resting conditions and perhaps only insignificantly data taken at lower work levels, and hence do not explain why the pulse rate at rest (sitting for man, standing for horse) is so much higher in De Mar, a marathon runner in good condition, than in average horses.

REFERENCE BASE AND SIZE EQUIVALENCE

While animals of different size may be equalized with respect to metabolic rate by adopting oxygen consumption rate during rest as a base value, such equalization cannot be made for pulse rate. The reason that pulse rate during rest can not be taken as a base value for equalizating animals of different size with respect to pulse rate consists in the fact that pulse rate is partially dependent on training and physical condition.[13-18] Oxygen consumption rate, on the other hand, is apparently not altered by training.[15,18-20]

How does training, which tends to lower the heart rate, influence the capacity of the cardio-respiratory system as exhibited by the acceleration of the heart during work? Schneider[21] cited reports[22] indicating that on a percentage basis the heart of an athlete accelerates as fast with work as does that of a non-athlete. Computing acceleration on a percentage basis, however, penalizes the athlete for his lowered pulse rate, since if training reduces the resting pulse rate from 70 to 50, then an absolute increase of 10 beats per minute due to exercise, as computed on a percentage basis, amount to 14 per cent before training or 20 per cent following training.

12Du Bois, E. F., Basal Metabolism in health and disease, Lea & Febiger. 1936, Philadelphia.

13Benedict, F. G., and Carpenter, T. M., Carnegie Inst. of Washington, Pub. 126, 236, 1910.

14Steinhaus, A. H., Am. J. Physiol. **76**, 184, 1926.

15Schneider, E. C., Clarke, R. W., and Ring, G. C., Am. J. Physiol. **81**, 255, 1927.

16Robinson, S., Edwards, H. T., and Dill, D. B., Science, **85**, 409, 1937.

17Robinson, S., Harmon, P. M., Am. J. Physiol. **133**, 168, 1941.

18Knehr, C. A., Dill, D. B., and Neufeld, W., Am. J. Physiol. **136**, 148, 1942.

19Steinhaus, A. H., Physiol. Rev. **13**, 129, 1933.

20White, P. D., J.A.M.A. **120**, 642, 1942.

21Schneider, E. C., Physiology of muscular activity, W. B. Saunders Co., p. 270, 1936.

22Henderson, Y., Haggard, H. W., and Dolley, F. S., Am. J. Physiol. **82**, 512, 1927.

On an absolute basis, the acceleration of the pulse rate of the athletic De Mar is somewhat lower than that of the non-athletic C.V.C. and D.B.D., as shown by the slopes of the equations of Fig. 3. The lines for the horses in the two lower sections of the figures all have about the same slope. Since the pulse rate cannot be expressed on a relative basis as was done for oxygen consumption in Fig. 3 without making it appear that the heart rate accelerates more rapidly with work in the fit than in the unfit, some other approach towards developing a relative index is indicated.

It is generally known that small animals have faster pulse rates than large animals. Clark[23] cited pulse frequencies from 730 in the mouse to 39 in the horse. He found that for a wide range of data, pulse rate varies inversely with body weight raised to a fraction power. If body weight is expressed in kilograms (instead of in grams as given by Clark) his equation[23] relating pulse rate, f, with body weight, W, may be written:

$$f = 217W^{-0.27} \quad \text{......(2)}$$

Kleiber,[24] too, correlated pulse rate with body weight, and in data for five species by Rihl[25] computed an approximate fractional power of —1/4.

It has likewise been established that for interspecies data basal oxygen consumption varies with a fractional power of body weight, with approximately[26,27] $W^{0.73}$, as indicated by the equation

$$O_2 = 10.2W^{0.73} \quad \text{......(3)}$$

in which O_2 is oxygen consumption in cc/min. and W is weight in kilograms. Equation (3) would likewise apply to "resting" (in contrast to basal) oxygen consumption if an appropriate change is made in the proportionality constant, as we[28] have found in growing rats, for example, a parallelism between basal and "resting" metabolism.

Dividing equation (3) by equation (2), we obtain the oxygen consumption per pulse beat, or the oxygen pulse, given by the equation

$$\text{Oxygen pulse} = \frac{O_2}{f} = \frac{10.2W^{0.73}}{217W^{-0.27}} = 0.047W^{1.00} = \text{approximately } 0.05W \quad (4)$$

Equation (4) shows that for interspecies data, oxygen pulse is directly proportional to body weight.

We further confirmed this relation by fitting an equation to the data from the literature given in Table 2. For these data, which we

[23]Clark, A. J., Comparative physiology of the heart, p. 143, The Macmillan Co., New York, 1927. Clark's equation, p. 89, is Pulse rate = 1400/(body weight, gms.)$^{0.27}$.
[24]Kleiber, Max, Hilgardia, 6, 315, 1932.
[25]Rihl, J., Handb. d. Norm. u. Pathol. Physiol. 7 (1), 449-522, 1927.
[26]Brody, S., and Procter, R. C., Missouri Agr. Exp. Sta. Res. Bul. 166, p. 89, 1932.
[27]Brody, S., Procter, R. C., and Ashworth, U. S., Id., Res. Bul. 220, p. 11, 1934.
[28]Kibler, H. H., and Brody, S., J. Nutr. 24, 461, 1942.

TABLE 2.—INDICES OF WORK CAPACITY FOR DIFFERENT SPECIES

Species	Work capacity index: Oxygen pulse cc. O_2/pulse	Work capacity index: O_2 pulse / Kg.	Data and source from which the indices at left were computed: Body wt. Kg.	Pulse rate per min.	O_2 consumption cc./min.#	Reference
Mouse, "tame"	0.0024	0.096	0.025	600	1.45	1 & 2
Rat, "tame"	.015	.075	.200	440	6.57	1 & 2
Guinea pig	.020	.050	.400	267	5.44	2
Rabbit, "tame"	.073	.037	2.0	205	15.0	2
Rabbit	.094	.036	2.6	180	16.9	3
Cat	.230	.092	2.5	122	28.6	2
Marmot	.136	.051	2.6	80	10.9	3
Dog	.52	.080	6.5	120	62.2	2
Dog	.80	.083	9.6	96	76.4	2
Dog	1.44	.072	20	85	122	2
Goat	1.43	.040	36	81	116	3
Goat	1.75	.053	33	135	236	2
Goat, Female	2.98	.060	50	80	238*	4
Sheep	2.15	.048	45	78	168	3
Sheep	2.64	.053	50	75	198	2
Sheep, Male	4.60	.052	88	72	331*	4
Woman	2.74	.049	56	66	181	3
Man	3.95	.061	65	60	237	3
De Mar (athletic)	5.0	.081	61.5	52.1	262*	5
C. V. C (sedentary)	3.2	.054	59.0	76.6	248*	5
D. B. D. (sedentary	4.2	.059	71.5	58.2	246*	5
Shetland ponies	22.6	.080	284	42.9	971*	Table 1
Percheron horses	53.1	.082	646	42.8	2271*	Table 1
Beef cow	23.7	.052	457	60	1420*	4
Steer	33.5	.046	730	48	1606	6
Elephant	302.0	.082	3672	31	9377*	7

#Many of the values in this column were computed from metabolism data, Cal/24 hrs., by assuming that 4.8 Calories is the heat equivalent for 1000 cc. of oxygen.

*Non-basal data. Further investigation is needed to study the influence of fasting and other factors on work-capacity indices.

1. Clark, A. J., Comparative Physiology of the Heart, pp. 143-145, The Macmillan Company, New York, 1927.
2. Cited by Clark (reference 1, above) from the literature.
3. Benedict, F. G., Carnegie Inst. Wash. Pub. 503, pp. 62, 176, 1938.
4. Unpublished Missouri data.
5. Bock, A. V., Vancaulaert, C., Dill, D. B., Folling, A., and Hurxthal, L. M., J. Physiol. 66, 136, 1928.
6. Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. 377, pp. 226, 227, 1927.
7. Benedict, F. G., Carnegie Inst. Wash. Pub. 474, pp. 128, 268, 1936.

plotted in Fig. 4, we obtained the equation

$$\text{Oxygen pulse} = 0.06\ (\text{body weight, Kg.})^{0.99}$$

The fact that Table 2 included some data measured under non-basal conditions may account for the fact that the proportionality factor is closer to 0.06 than to 0.05 as found in equation (4).

The oxygen pulse was defined by Henderson and Prince[29] as "the amount of oxygen consumed by the body from the blood of one systolic discharge of the heart," and they concluded that "the oxygen pulse more than any other factor determines the total energy which a man can command for the most strenuous moments of life." The demonstration (eq. 4) that oxygen pulse is directly proportional to body weight for a wide range of interspecies data should enhance the importance of this index.

29Henderson, Y., and Prince, A. L., Am. J. Physiol. 35, 106, 1914.

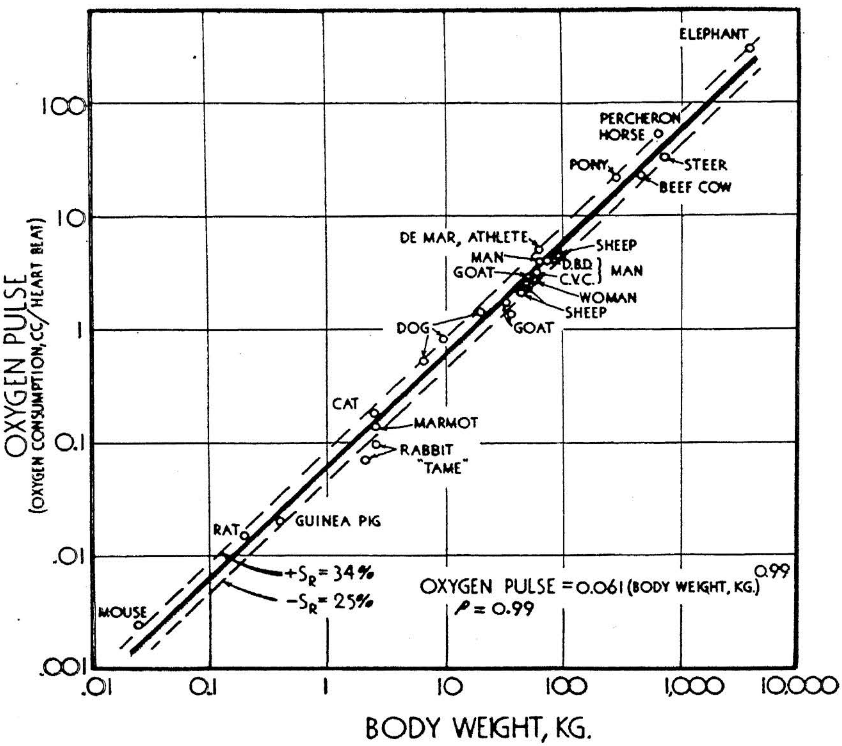

Fig. 4.—Oxygen pulse (oxygen consumed per beat of the heart) plotted against body weight on logarithmic paper (data from Table 2). The equation was fitted by the method of least squares and is represented by the heavy line. The slope of the line is approximately 1, demonstrating that oxygen pulse is directly proportional to body weight in animals of different species. The dash lines represent the standard errors of estimate; part of the variability between species is due to differences in cardio-respiratory capacity and part to differences in experimental conditions. P represents the coefficient of correlation.

Values of oxygen pulse are plotted for horse and man during rest and work in Fig. 5. The relative magnitude of this index in interspecies data is dependent on body weight, but the greater rise of oxygen pulse with increase in oxygen consumption in horse as compared to man may be attributed, in part, to differences in experimental conditions.

Equation (4) may be changed to the form

$$O_2 = 0.05Wf \qquad (5)$$

which indicates that the O_2 consumption is directly proportional to the product of body weight and pulse rate in interspecies data.

Fig. 6 shows the applicability of equation (5) to our data on horses. Data for oxygen consumption and pulse rate during rest from Table 1A are plotted against body weight on logarthmic paper. Equations (2) and (3), previously discussed, are likewise shown for com-

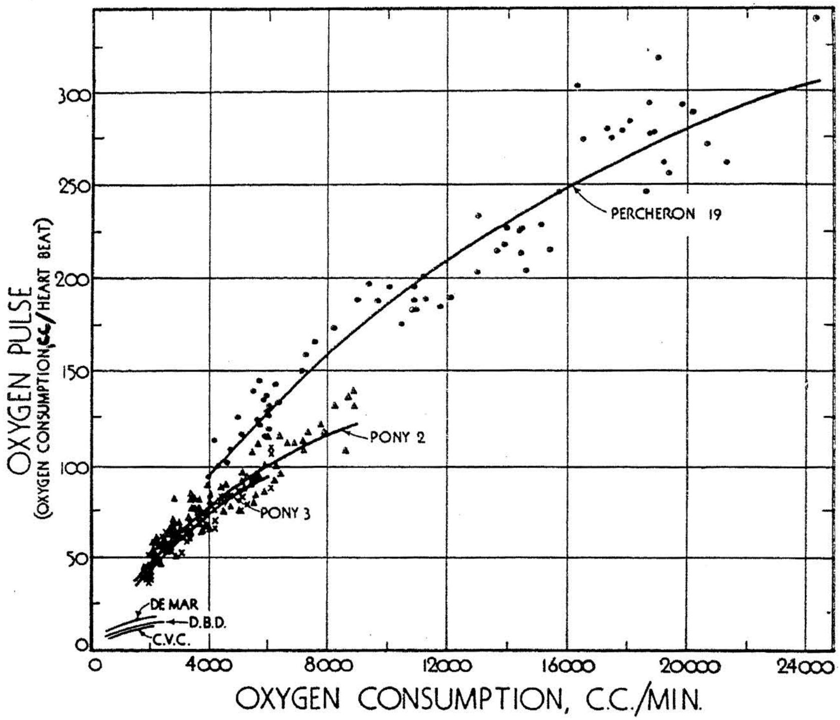

Fig. 5.—Oxygen pulse plotted against total oxygen consumption.

parative purposes. Pulse rate is shown to be constant for horses of all weights (pulse rates during rest are given in Table 1 and pulse rates during work in Table 3). Since pulse rate, f, is independent of body weight in horses, it would follow from equation (5) that oxygen consumption in these horses must be directly proportional to body weight. This direct proportionality between oxygen consumption and body weight in horses is in decided contrast to the fractional power relationship in interspecies data, but is verified by our fitted equation

$$O_2 = 3.45W^{1.01}$$

Benedict[30] citing unpublished data by Ritzman, also reported an approximately constant metabolism per unit weight in mature horses of different size.

Buchanan[31] has pointed out the reciprocal relation of pulse rate and the ratio heart weight/body weight. Active animals or species with a large heart in relation to their body weight have a relatively

[30]Benedict, F. G., Carnegie Inst. Washington Pub. 503, p. 143, 1938.
[31]Buchanan, F., Science Progress 5, 60, 1910.

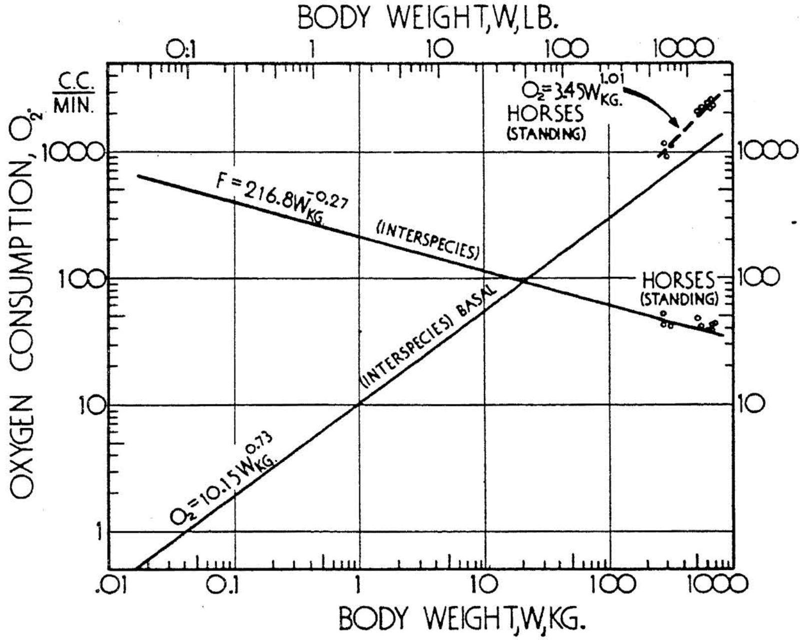

Fig. 6.—Oxygen consumption and pulse rate as functions of body weight. The horse data are taken from Table 1.

low pulse rate, while those with relatively small hearts have faster pulse rates. Clark[23] has shown that the increase in heart weight with body weight is less rapid within than between species. We[32] found that heart weight varies with the 0.98 power of body weight in mature animals of different species over a range of body weights from 0.01 to 100,000 Kg. These considerations, suggest that if equation (5) is to be used to estimate basal oxygen consumption, increased precision may be obtained by allowing for variations in heart ratios. Heart size and stroke volume in the living animal can now be estimated by teleoroentgenographic[33] and roentgenkymographic[34] methods.

Equation (4) may also be written in the form

$$\frac{O_2}{W} = 0.05f \qquad (6)$$

indicating that oxygen consumption, O_2, per unit weight, W, is directly proportional to pulse rate, f, in interspecies data. The preceding remarks concerning the precision of equation (5) apply also to equation (6).

32Brody, S., and Kibler, H. H., Missouri Agr. Exp. Sta. Res. Bul. 328, 1941.
33Master, A. M., Dack, S., and Jaffe, H. L., J.A.M.A. 120, 1271. 1942.
34Keys, A., and Friedell, H. L., Am. J. Physiol. 126, 741-752, 1939.

Finally, equation (4) may be written in the ratio form

$$\frac{O_2/f}{W} = 0.05 \quad \text{...(7)}$$

indicating that basal oxygen pulse per unit body weight is a constant for interspecies data. The constant 0.05 is the average value of basal oxygen pulse per kilogram of body weight for all species; for individual animals or species, the ratio oxygen pulse per kilogram of body weight varies above and below this average. The higher this ratio, the greater is the work capacity of the animal. This ratio (eq. 7), oxygen pulse per unit body weight, is, therefore, the index of work capacity which we have been seeking; it is a measure of muscular-work capacity independent of body weight. The precision of this index is not affected by the reciprocal relation between pulse rate and heart ratio, since the value of the index is increased when the pulse rate is low (high heart ratios are associated with high work capacity).

Table 2 illustrates the applicability of these indices to interspecies data. Oxygen pulse, which is directly proportional to body weight (eq. 4), increases from 0.0024 cc. in the mouse to 302 cc. in the elephant. Oxygen pulse/Kg., on the other hand, is independent of body weight and varies with muscular work capacity and physical fitness. High indices of 0.07 to 0.09 are usual in athletes, horses, and dogs in contrast to low indices of 0.03 to 0.05 in sedentary men, women, sheep, and domestic rabbits.

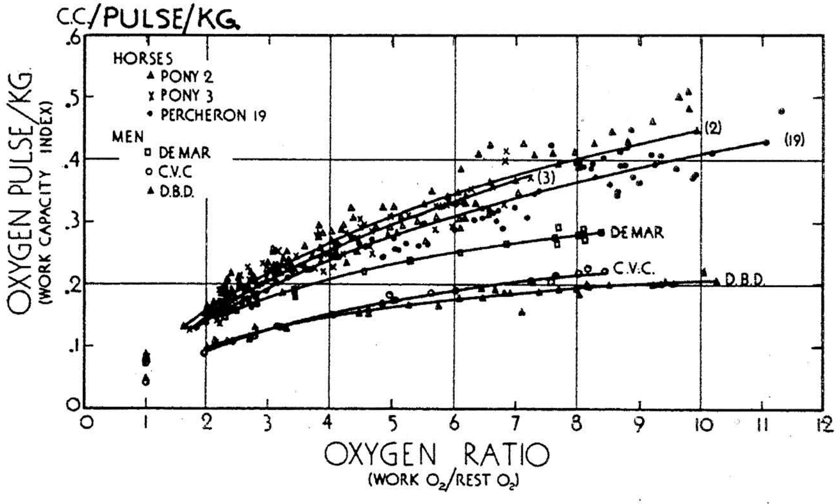

Fig. 7.—Oxygen pulse per kilogram of body weight, an index of cardio-respiratory capacity, plotted against oxygen ratio, an index of energy expenditure, during rest and work.

TABLE 3.—INDICES OF WORK CAPACITY DURING REST AND WORK IN HORSE AND MAN
(Derived From Equations Given in Fig. 3)

Energy expenditure (oxygen ratio)	Subject					
	Pony 2	Pony 3	Percheron 19	C.V.C.	D.B.D.	De Mar
	Oxygen Consumption, cc/min.					
1*	908	898	2159	248	246	262
2	1816	1796	4318	496	492	524
3	2724	2694	6477	744	738	786
4	3632	3592	8636	992	984	1048
5	4540	4490	10795	1240	1230	1310
6	5448	5388	12953	1488	1476	1572
7	6356	6286	15112	1736	1722	1834
8	7264	7184	17271	1984	1968	2096
9	8172	....	19430	2232	2214	2358
10	....	....	21589	....	2460	....
	Pulse Rate, Beats/min.					
1*	38.1	41.5	39.6	76.6	58.2	52.1
2	42.1	45.4	43.5	88.0	70.2	61.8
3	46.2	49.4	47.4	99.4	82.3	71.5
4	50.2	53.3	51.3	110.8	94.3	81.2
5	54.2	57.2	55.2	122.2	106.4	90.9
6	58.2	61.1	59.1	133.6	118.4	100.6
7	62.3	65.1	63.1	145.1	130.5	110.3
8	66.3	69.0	67.0	156.5	142.5	120.0
9	70.3	...	70.9	167.9	154.6	129.6
10	...	...	74.8	....	166.6	....
	Oxygen Pulse (Absolute Index of Work Capacity)					
1*	24	22	54	3.2	4.2	5.0
2	43	40	99	5.6	7.0	8.5
3	59	55	137	7.5	9.0	11.0
4	72	67	168	9.0	10.4	12.9
5	84	78	196	10.0	11.6	14.4
6	94	88	219	11.1	12.5	15.6
7	102	97	240	12.0	13.2	16.6
8	110	104	258	12.7	13.8	17.5
9	116	...	274	13.3	14.3	18.2
10	...	...	289	...	14.8	...
	Oxygen Pulse/Kg. (Comparative Index of Work Capacity)					
1*	0.088	0.083	0.076	0.054	0.059	0.081
2	.158	.151	.140	.095	.098	.138
3	.216	.208	.193	.127	.126	.179
4	.264	.253	.237	.153	.145	.210
5	.308	.294	.276	.169	.162	.234
6	.344	.332	.309	.188	.175	.254
7	.374	.366	.339	.203	.185	.270
8	.403	.392	.364	.215	.193	.285
9	.425	...	.386	.225	.200	.296
10	...	...	.408	...	.207	...

*Energy expenditure is given in multiples of resting oxygen consumption (resting oxygen consumption = 1).

Since completing Table 2 we have come across data on three Yale oarsmen by Henderson and Haggard.[35] When we computed work capacity index values for these oarsmen we found values around 0.09 for two of the crew, but a value between 0.05 and 0.06 for the third, the number 7 crew member.

The data and curves of Fig. 7 appear to justify the general validity of the indices developed. Oxygen pulse/Kg., the index of work capacity

[35] Henderson, Y., and Haggard, H. W., Am. J. Physiol. 73, 193, 1925.

is plotted against oxygen ratio, the index of physiological energy expenditure. On this basis, De Mar, the athlete, compares favorably with the horses for resting and lower work levels where differences in experimental conditions have little effect (Table 3). It appears that man and horse in good physical condition have an oxygen pulse/Kg. index during rest of 0.07 to 0.09 and that index values around 0.04 to 0.06 can be expected in subjects with sedentary habits.

Index values derived from resting data are not necessarily evidence of work capacity. It is the cardio-respiratory behavior under stress that indicates an animal's reserve power. Schneider and Truesdell,[36] for example, in testing 2,000 aviators found a greater variability in their pulse rate for standing than for lying. They also cite abnormally rapid pulse rates in patients, standing, who had normal rates while lying. It seemed desirable, therefore, to compute the values of oxygen pulse/Kg. for increasing levels of energy expenditure (Table 3) to see whether differences found between subjects at rest were maintained during increasing exertion. Differences in experimental conditions make comparison between man and horse impracticable for high work levels, but intraspecies comparisons (Fig. 7) exhibit only one crossing of curves, the curve of C.V.C., rising slightly above that for D.B.D. at higher work levels.

When oxygen pulse/Kg., an index of work capacity, is plotted (Fig. 7) against oxygen ratio, a measure of bodily energy expenditure, changes in cardio-respiratory capacity may be studied for increasing levels of bodily stress. The divergence of the curves for the horses from those for the men may be largely attributed to experimental differences as previously explained. The degree of parallelism in the curves for each species indicates that for the subjects studied, the indices for *resting conditions* give a fairly reliable indication of work capacity. The crossing of the curves of C.V.C. and D.B.D., is, however, indicative of the greater value of *working* tests.

SUMMARY AND DISCUSSION

We have taken the amount of oxygen consumed per beat of the heart and per kilogram of body weight as a measure of cardio-respiratory capacity as, perhaps, the best index[37] of muscular work capacity in warm blooded species. Our measurements are expressed in terms of *oxygen pulse per kilogram of body weight,* cc/beat/Kg.

[36]Schneider, E. C., and Truesdell, Dorothy, Am. J. Physiol. 61, 429, 1922.

[37]Pulse rate/(body weight)$^{-0.27}$ might be used as an index of work capacity (low values indicating high work capacity) since this ratio is constant, on the average, for animals of different size (eq. 2). We have tried this index, however, and have found that it indicates that in respect to work capacity, horses are no better than guinea pigs, dogs no better than marmots, and elephants no better than sheep.

This index is, apparently, not affected by body size; approximately the same value for this index was computed (Table 2) in animals ranging in size from mouse to elephant. Variations in this index for basal or resting conditions usually represent differences in cardio-respiratory capacity. De Mar, a marathon runner, for example, had an index of 0.08—as high as we found for our work horses—in contrast to an index of 0.05 in non-athletic C.V.C.

Measurements of cardio-respiratory capacity at *rest* are usually but not always reliable indices of *work* capacity. When we computed index values for three members of a Yale crew for resting conditions from oxygen consumption and pulse rate data reported by Henderson and Haggard,[35] we found values around 0.09 for two of the crew, but a value between 0.05 and 0.06 for the third, the number 7 crew member. Was the low value for this athlete a normal variation (excitement or slight physical disturbances at the time of the test could have altered the relation between pulse rate and oxygen consumption) or was this number 7 crew member able to compete in this strenuous sport despite a relative low index of work capacity by reason of a superior drive to win, coupled perhaps with exceptional ability to go into oxygen debt (need for extra O_2 as a result of accumulation of lactic acid and related products during work)?

Such a question cannot be answered by a study of indices for *resting* conditions; more information may be obtained by a study of the behavior of the index under *working* conditions. When index values for horses and men are plotted against bodily energy expenditure (bodily energy expenditure during work being measured by the rate of oxygen consumption, and made equivalent for animals of different size by dividing oxygen consumption rate during work by oxygen consumption rate during rest), they rise with the level of exertion and trace out characteristic curves for each individual horse and man (Fig. 7). These curves for work may be called working-index characteristics in contrast to resting-index characteristics.

Working-index characteristic curves such as we have plotted for horses and men should prove very useful for clinical purposes and in determining, as in the case of the crew member 7, whether an athlete's performance is due to mistaken ambition, requisite physical capacity, or to some other compensation ability. Such curves should prove useful tools to the geneticist for measuring trends in breeding programs and in discovering exceptional abilities in individual animals.

Our use of oxygen pulse per kilogram weight as a measure of cardio-respiratory capacity, which is independent of body size, is based on our demonstration (Fig. 4 and eq. 4) that oxygen pulse is directly proportional to body weight. Other interesting implications follow from this relation; basal metabolism per unit body weight must be directly proportional to pulse frequency, and total metabolism must be directly proportional to the product of body weight and pulse rate. In horses we found that pulse rate was approximately constant for different body weights, and that consequently metabolism during rest was directly proportional to body weight.

These average relations between metabolism, pulse rate, and body weight are modified in particular cases, it appears, by the ratio of heart weight to body weight. Especially active species have disproportionately large hearts and relatively slow pulse rates. The ratio of heart weight to body weight, the heart ratio, therefore, enters as a fourth factor in the determination of metabolism from body weight and pulse rate data.

The precision of the index oxygen pulse per kilogram of body weight as a measure of cardio-respiratory capacity is not affectd by variations in heart ratios. The quantity of blood that the heart pumps per beat is a major factor in determining cardio-respiratory capacity, and Table 2 shows that large-hearted species, such as the horse and dog, have high indices. The quantity of blood expelled by the heart each beat is not solely a function of heart size. The heart of an athlete contracts more strongly and empties more completely at each beat than the heart of a non-athlete.

Basal or resting tests may indicate cardio-respiratory capacity for the resting condition only, especially in cardiac patients, rather than potential cardio-respiratory capacity during work; but it is reserve capacity that determines work capacity. The mouse at rest has a high index (Table 2), but working index characteristic curves might prove the mouse to have very little reserve capacity. To obtain a complete evaluation of cardio-respiratory capacity, especially in unusual cases, indices for both resting and working conditions should be determined.