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COLLEGE OF AGRICULTURE

AGRICULTURAL EXPERIMENT STATION RESEARCH BULLETIN 179

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XXV. The Course of Energy and Nitrogen Meta bolism in the Domestic Fowl During 48-Day Fasts. With special reference to temperament and training of the birds. Notes on 60-day fasts in swine.

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FOREWORD

The special investigation on growth and development is a cooperative enterprise in which the departments of Animal Husbandry, Dairy Husbandry, Agricultural Chemistry, and Poultry Husbandry have each contributed a substantial part. The plans 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 represented by Dr. R. W. Thatcher, who has given valuable advice from the beginning of the investigation.

F. B. MUMFORD, Director Agricultural Experiment Station.

ACKNOWLEDGMENTS

Acknowledgments are made to Mr. R. C. Procter for preparing the charts and tables. This research was carried out in the Department of Agricultural Chemistry, of which Dr. A. G. Hogan is the chairman.

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

XXV. The Course of Energy and Nitrogen Metabolism in the Domestic Fowl During 48-Day Fasts. With special reference to temperament and training of the birds. Notes on 60-day fasts in swine.*

VIRGIL W. PHILLIPS, URAL S. ASHWORTH, SAMUEL BRODY

ABSTRACT

Two yearling domestic fowls (White Rock breed) were fasted until death (water and sand were available); and a third hen was given 50 gram per day of a nitrogenfree diet until death. These birds survived, respectively, 48, 40, and 23 days, declining in weight, respectively, from 1840 to 690, 1974 to 776, and 1982 to 1341 grams. Their energy metabolism ("basal metabolism") was measured daily by a volumetric, and also by Haldane's gravimetric method. Their combined daily urinary and fecal nitrogen, as also total creatinine, were measured daily. Mathematical (mainly graphic) analyses are presented of the time relations of the metabolic and body weight changes. Similar analyses are presented of published fasting data of humans and dogs, and the results are compared. Some striking differences were thus found between our data on the domestic fowl and the published data on humans and dogs. The "basal metabolism" data by the volumetric and gravimetric method appear to agree within the limits of experimental error inherent in the experimental subjects. The well-trained bird gave the most consistent results. The well-trained bird gave the most consistent results. The well-trained bird gave the most consistent results. The well-trained bird also survived longest, indicating the influence of training and temperament on the survival period in fasting. A minimum energy metabolism of about 400 Calories per square meter, or about 35 Calories per kilo was found on the 20th day of fast in the domestic fowl. The minimum nitrogen excretion is about 165 mg. total nitrogen per kilo per day on the twelfth day of fast, and about 12 mg. total creatinine per kilo per day at the same time. Data are also presented on energy and nitrogen metabolism during 2-month fasts in two sows.

I. INTRODUCTION

Fasting, that is, complete abstinence from food, of course involves living on the accumulated reserves in the body. An animal in a very fat and well developed condition can maintain a fast without fatal results for a very much longer period than a thin, or poorly developed, animal. The Alaskan fur-seal bull, for example, fat and sleek in May, has no difficulty in maintaining a complete fast during the entire breeding season, lasting two to three months, and in the same time ward off rivals from his herd of cows. The complete fast of many weeks, or perhaps months, of the salmon on his way upstream to the breeding grounds, is another spectacular example of the same type.

In addition to the physiologically normal types of fasting of which the above are examples, there are any number of pathological types of fasting, when the individual can not feed, or digest, or assimilate, or properly utilize nourishment. And, of course, it is easy to think of partial or complete types of fasting due to unfavorable environmental conditions such as famines, wars, social and economic upheavals in human society; or drought, rigors of winter, insect afflictions, in the case of other species. And there are, then, the spectacular religious, political, and psychopathic fasts; widely known examples of the former are the fasts of Gandhi and MacSwiney.

II. OBJECTS

From one point of view, fasting is a very simple kind of nutrition; simple in the sense of not being complicated by the intake of food from external sources with the associated phenomena of digestion, assimilation, etc. One of the objects of the present research is to investigate metabolism under the simplifying conditions of fasting.

The fasting of an animal involves a number of questions. Some of these are: (1) What is the course of metabolism with the increasing time of fasting? (2) What are the changes in the relative contributions of proteins and fats towards supplying energy to the organism with the advance of the period of the fast? (3) What is the relative economy with which the dwindling energy and nitrogen resources are utilized by the animal in the various stages of fasting? (4) What is the percentage of body weight loss in a fast leading to a fatal issue? (5) What is the survival period in a complete fast, and how does temperament influence it? We had all these objectives in mind, and this paper is a preliminary and tentative report on the work done in this connection.

The immediate incentive to this work is due to the fact that in April, 1930, a hen was fasted for 15 days in connection with a test on the reliability of a volumetric method for measuring oxygen consumption. The results, which turned out to be rather erratic, were published as a matter of record, but without comment, on p. 179, of Missouri Research Bulletin 143. The volumetric method employed at the time is described on page 18 of the same bulletin. It seemed desirable to repeat this work by this volumetric method, and check it with Haldane's gravimetric method, in order to find out whether the said erratic results were due to the unreliability of the volumetric method as such, or to the individuality (including temperament) of the bird. Incidentally, in this research, the excreta were collected and analyzed for nitrogen and total creatinine so as to throw light on some of the other objectives enumerated above.

III. METHODS

As previously indicated, the domestic fowl was used as experimental subject. Three birds were included in this preliminary research. To determine the influence of temperament and training, one of the birds (No. 11) was raised in the laboratory, thoroughly habituated to being handled and having its metabolism measured. The other two birds (1040 and 980) were taken directly from the poultry farm, with no

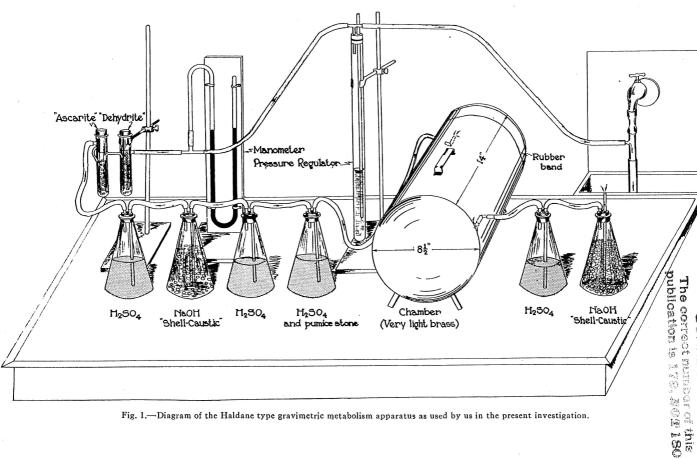


Fig. 1.—Diagram of the Haldane type gravimetric metabolism apparatus as used by us in the present investigation.

ONNECTOR

previous "laboratory experience" except a 5-day preliminary feeding and metabolism period.

The volumetric method employed was the same as that used in 1930 (pp. 18 and 12, Missouri Research Bulletin 143, and pp. 67-70, Missouri Research Bulletin 166). The Haldane gravimetric apparatus that we used is illustrated in Fig. 1.

The excreta were collected on the floor, which was a large pane of glass. The excreta were carefully removed at 24-hour intervals, and analyzed for total N by the usual Kjeldahl method and for total creatinine by Folin's method. In the original data the nitrogen was divided into two parts, that soluble in water (Sol. N) and the residual (insol N).

All three hens had access to water and to sand. Birds 11 and 1040 had no access to food, but bird 980 was force-fed 50 grams a day of a nitrogen-free diet, which was thought to cover its energy and vitamin needs. The N-free ration of 980 consisted of starch 74, sucrose 10, salts 4, cellulose 2, butterfat 8, cod liver oil 2, and 2 c. c. per day of tikitiki.

The birds were kept and measured in a room having a temperature range between 25° and 30° C. (during July and August, 1932).

IV. RESULTS

1. Hen Number 11.—As previously noted, Hen 11, was thoroughly habituated to the laboratory, to being handled, and to having her metabolism measured. In brief, she had, for this purpose, a satisfactory "temperament" which may have been largely acquired by her experience.

She survived 49 days without food. (Kuckein's fowls fasted 10 to 13 days.) This compares favorably with Awrorow's four dogs which survived 17, 45, 60, and 66 days, the duration of survival depending apparently on age and temperament of the animal, as well as on its stores of fats. It, of course, falls far short of the longest fasts on record for dogs, namely 117 and 104 days recorded by Howe, Mattill, and Hawk on their Scotch collie dog Oscar, which, however, weighed 3 to 4 times as much as Awrorow's dogs. Other conditions being the same, it appears that the larger the animal, the greater its survival period; that is inferred from the fact that the metabolism per unit weight decreases with the size of the animal, and that the maximum percentage loss in weight is nearly the same in Howe's dog (nearly 63%) as in Awrorow's dog No. 4 (over 61%) Our hen No. 11 likewise lost over 61% (1840 gm. at beginning of fast, 690 gm. after death), from which it may be tentatively concluded that the maximum weight loss (as computed in the customary arithmetical manner) that can be borne by a warm-blooded animal is of the order of 60 to 65%.

The essential energy and nitrogen metabolism data on hen No. 11 are shown in Fig. 2 and Table 1.

The left column of charts in Fig. 2 plotted against time of fast represents, respectively, reading from bottom to top: Total Calories per day, Calories per sq. meter per day, and Calories per kilo per day. The uppermost chart represents Calories per kilo per day plotted against body weight. The light circles represent the measurements by the

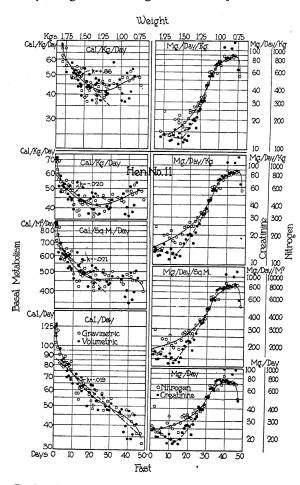


Fig. 2.—The course of energy and nitrogen metabolism in Hen 11 with the advance of the period of fasting. The column of curves on the left represents energy metabolism (light circles for the Haldane gravimetric method; solid circles for the simple volumetric method). The column of curves on the right represents total nitrogen (light circles) and total creatinine (solid circles) excretion. The broken curves on the left are straight lines giving the approximate slope (k) of the decline. The value of the slope, 0.02, indicates that the decline in energy metabolism is (following the 3rd day) of the order of 2 per cent per day.

Haldane gravimetric method, while the solid circles represent the results of the volumetric meth-

The right column of charts in Fig. 2, represents in a similar manner total nitrogen and total creatinine excretion.

The results in Fig. 2 and Table 1 may be summarized as follows:

Under the given conditions the agreement between the volumetric and gravimetric methods for energy metabolism is satisfactory. Ten per cent deviations between the methods on given days are frequent, but they are not systematic. differences may be due to the fact that the measurements by two methods were necessarily different made at times of the day

with associated differences in the degree of relaxation of the bird, and also to differences in the duration of confinement by the two methods.

The birds were confined for from 30 to 60 minutes by the volumetric method, and two hours by the gravimetric method.

Table 1.- Metabolism Data for Hen No. 11

Fast Days	Body Wt. Gms.	Cals./day Volumetr. Method	Cals./day Gravimetr. Method	Ratio Vol. to Gravim.	Total N Excret. mg./day	Total Creatinine mg./day	Cals. From Prot.	Ratio Cals. from Prot. to Total Cals.* %
123456789011234567890123222456789012334567890123345678901233456789012344567890123445678901234456789012334567890123456789012345678901233456789012345678901234445678901234678901200000000000000000000000000000000000	1840** 1790 1670 1650 1620 16600 1580 1560 1540 1530 (1510) 1470 1450 1430 1330 1340 1330 1330 1310 1280 (1265) 1230 1230 1180 1180 1160 (1137) (1070) 1050 1020 (1000) 980 9870 870 870 870 730	127.6 899.3 884.5 99.3 884.5 91.9 664.4 072.1 664.3 664.4 072.1 664.3 66	112.6 108.3 85.9 79.4 881.4 881.4 881.4 63.0 63.0 65.7 651.6 60.8 60.8 60.8 60.8 60.8 60.8 60.8 60	113.3 82.5 103.0 106.7 90.0 88.3 96.9 85.6 101.3 (100.0) 81.5 100.5 102.5 119.6 81.7 102.5 105.4 (100.0) 81.7 102.5 105.4 88.6 90.5 (100.0) 128.2 (100.0) 128.2 (100.0) 128.2 (100.0) 106.1 81.7 79.2 110.6 81.7 100.0 81.7 100.0 10	266 420 230 230 231 235 317 (255) 312 284 337 (2286 (298) 340 3323 344 337 348 376 415 507 535 (570) (605) (643 (670) (609) 782 (710) (733 713 713 713 713 713 713 713 713 713	24.0 25.0 20.5 20.5 20.5 22.5.4 (21.0) 17.6 18.5) 17.6 18.5) 17.6 22.0 (19.0) 17.6 22.0 (21.5) 25.8 27.1 26.8 27.1 26.2 21.6 21.6 21.6 21.6 21.6 21.7 25.8 27.1 26.9 21.6 21.7 25.0 (50.5) (60.5) (60.5) (76.0) (77.0 (78.0) (77.0 (78.0) (7	7.1 11.1 6.1.1 6.1.1 6.1.2 4.8 8.3 5.9 9.6 6.7 7.7 6.2 6.8 7.7 9.8 9.8 9.8 10.1 11.0 11.0 11.1 11.1 11.1 11.1 11	10.8 6.6 6.9 7.4 10.9 10.9 11.3 10.9 11.3 11.4 19.9 11.3 11.3 11.3 11.3 11.3 11.3 11.3

In order to determine the influence of the duration of confinement on the metabolic rate, Hen 1040 was confined in our volumetric-method chamber for 3 hours, and 15-minute graphic records were taken during the entire 3-hour period. The metabolic rates for the successive 15-

^{**}Assumed normal weight.
*Ratios were computed on basis of interpolation from the smooth curves of these data rather than
from numerical values given in this table. One gram of urinary nitrogen is taken to represent 26.51

Total Loss in live weight, 1110 grams; percentage loss in live weight, 60.3%.

Total heat production for volumetric method and gravimetric method is 2763 and 2779 Calories,

respectively.

Total Nitrogen excreted, 21,375 milligrams; total creatinine excreted, 1960 milligrams (in 47 days)

minute periods were then plotted against time of confinement as shown in Fig. 3.

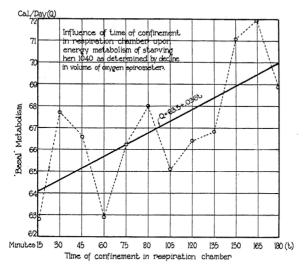


Fig. 3.—The influence of the duration of confinement of hen 1040 on her energy metabolism at successive 15-minute periods as determined by the volumetric-method respiration chamber system (for description of which see pp. 18 and 12, Mo. Res. Bull. 143, and pp. 67-70, Mo. Res. Bull. 166). The observed values are connected by broken lines; the smooth line represents a linear equation fitten by the method of least squares to all the data points.

Fig. 3 shows that during the first 60 minutes, the values ranged from 62.8 to 67.7 Calories (= $\frac{67.7-62.8}{65.2} \times 100 = 7.5\%$); during the second hour, they ranged from 63 to 68 (= $\frac{5}{65.5} \times 100 = 7.6\%$); during the third hour, they ranged from 66.3 to 72 Calories (= $\frac{5.7}{99.1} \times 100 = 4\%$). Taking the entire 3-hour period, the range is from 62.8 to 72 Calories (= $\frac{9.2}{67.4} \times 100 = 13.6\%$). If we fit a linear equation to the data (by the method of least squares), the range during the interval, as shown by the fitted line, is from 64 to 70 Calories which is 9% (= $\frac{6}{67} \times 100 = 9\%$).

Fig. 3 therefore suggests the following facts: First, the energy metabolism of the confined bird is not constant, but it fluctuates from period to period. The range of fluctuations between 15-minute periods in any one hour is of the order of 7%. If the periods were of shorter duration,

say 5-minutes instead of 15-minutes, then the range in fluctuations in an hour would be still greater. Second, the general apparent effect of confinement is to increase the metabolism with increase in the time of confinement (within the observed time interval of 3 hours). This is shown by the heavy line fitted to the data indicating a 9% increase in metabolism during the 3-hour period.

This would seem to explain the fact that our published values on metabolism of the domestic fowl (pp. 69-70, Missouri Res. Bul. 166, and p. 32, Missouri Res Bul. 176) are about 8% below those reported by Mitchell, Card, and Haines. Our previously published data are based on confinement periods of 15 minutes; and of the 15-minute record, a 5minute segment of lowest slope was used for computing the metabolism. Mitchell, Card, and Haines, on the other hand, confined their birds from 3 to 7 hours, and the metabolism was measured "during two or more 30-minute periods of quietness". Mitchell and Haines confined their birds from 22 to 23 hours. We feel that our data published in Missouri Research Bulletins 166 and 176, representing short periods of confinement, meet more nearly the definition of basal metabolism than do Mitchell's data based on long periods of confinement. In order, however, to assure thermal and gaseous equilibrium in the volumetric-method respiration-chamber system, we have computed the results (in the present experiment) on the basis of two 15-minute periods, provided that the temperature of the system remained constant within 1°C. during the entire period.

The above considerations lead us to say that we are satisfied that the extremely simple volumetric method of measuring metabolism is reliable. However, we feel it important that the period of measurement should be at least 30 minutes, and that the temperature of the system should be kept constant within 1°C. It is not practicable to correct for temperature changes in our volumetric-method system; and it is failure to give proper consideration to the temperature factor which led to the abnormally low values published on page 179, Missouri Res. Bul. 143.

Returning to Fig. 2, the lowest values per unit area appear to be about 400 Calories per square meter per day (assuming that Mitchell's modified surface area formula S. A. = 10.7W.656 is applicable to fasting birds). The lowest value for the metabolism per kilo is of the order of 35 Calories for this rather small bird (3/4 of the weight of the Rhode Island Hen reported on p. 179, of Missouri Res. Bul. 143).

As regards the nitrogen and total creatinine excretion, these decline somewhat for about 15 days from the beginning of the fast; they then rise in parallel fashion for about 20 days. They remain at an approximately constant level during the last ten days of the fast, followed by an abrupt decline on the last day, which may be due to retention of feces and urine.

The lowest nitrogen excretion is seen to be of the order of 165 milligrams of nitrogen per kilo body weight per day reached between the 12th and 15th day of fast; the highest values appear to be of the order of 870 milligrams reached in the last few days of fast.

The lowest total creatinine excretion appears to be of the order of 11 to 12, and the highest between 100 and 120 milligrams per kilo per day; the course of total creatinine and nitrogen follow nearly the same path throughout the course of the fast.

2. Hens 1040 and 980.—We next proceed to a consideration of hens 1040 and 980.

These birds differ from Hen 11, in that 11 was habituated to the laboratory, while 1040 and 980 were "wild", having been brought directly from a poultry farm especially for this experiment.

TABLE 2.—METABOLISM DATA FOR HEN No. 1040

THE TOTAL TO								
Fast Days	Body Wt. Gms.	Cals./day Volumetr. Method	Cals. /day Gravimetr. Method		Total N Excret. mg./day	Total Creatinine mg./day	Cals. from Prot.	Ratio Cals. from Prot. to Total Cals. %
Normal Normal Normal Normal Normal 1 2 3 3 4 5 6 7 8 9 10 111 113 114 115 116 117 118 119 221 222 224 225 226 227 228 229 331 335 336 337 338 340	1891	113.2 965.7 117.4 80.2 80.2 861.8 80.2 861.8 557.4 86.2 556.2 556.2 556.2 556.2 83.0 4 80.0 70.0 771.3 772.0 606.5 507.4 606.5 507.4 507.2 607.2	119.7 1104.5 1104.0 743.9 (74.0.0 767.7 89.0 767.7 69.1 890.2 81.6 890.2 81.6 890.2 81.6 890.2 81.6 890.2 81.6 890.2 81.6 80.0 81.6 80.0 80.0 80.0 80.0 80.0 80.0 80.0 80	94.6 89.8 101.1 107.6 116.8 125.5 (111.3) 77.3 72.8 84.8 54.2 74.8 60.4 62.1 (99.3) 143.7 (104.1) 129.6 89.2 109.9 (89.1) (100.0) (100	656 484 488 551 547 448 312 304 391 304 391 304 391 305 (450) 431 304 395 457 4090) 400 574 562 571 438 438 438 438 438 438 438 438	24.0 24.0 24.0 16.0 22.0 16.0 12.0 12.0 12.0 12.0 12.0 12.0 12.0 12.0 12.0 23.0 23.0 23.0 23.0 23.0 24.0 24.3 15.6 24.3 15.6 26.2 27.0 28.0 29.0 21.0 21.0 21.0 22.0 23.0 23.0 23.0 24.0 24.3 24.3 24.3 25.0 27.0 27.0 28.0 29.0 20.0 20.0 20.0 20.0 20.0 20.0 20.0 20.0 20.0 20.0 20.0 20.0 20.0	17.4 12.84) 18.46 14.59 61.99 61.93 10.47 9.10 10.12 11.60 11.73 11.40 12.77 11.40 12.77 11.52 11.70 11.52 11.70 11.52 11.52 11.52 11.53 11.52 11.53 11.52 11.53 11.53 11.54 1	10.9 11.7 (16.9) 16.9 18.1 10.6 (18.3) 12.4 (9.6) 11.9 14.3 (9.6) 11.0 12.4 (19.6) 14.1 (19.6) 14.1 (19.6) 14.1 19.7 14.8 11.9 14.8 11.9 14.8 11.9 14.8 11.9 14.8 11.9 12.9 13.0 14.1 14.1 16.9 17.7 18.1 19.9 19.0

Total loss in live weight, 1100 grams; percentage loss in live weight, 56.7%. Total heat production for volumetric method and gravimetric method is 2548 and 2726 Calories, respectively.

Nitrogen excreted, 17,274 mg.; creatinine excreted, 821 mg.

Hen 1040 was treated in the same manner as Hen 11. She had access to water and sand, but no food. Hen 980 was force-fed the nitrogen-free diet. Thus 980 was starved with respect to nitrogen only. It is interesting to note that 980, which had access to the N-free diet, died in 23 days, while 1040 which had no access to food at all, survived 41 days. 980 developed a severe case of polyneuritis by the 18th day on this diet. It is also interesting to note that rats survived in our laboratory for over 3 months (95 to 100 days) on the N-free diet we fed to hen 980.

The numerical data for 1040 and 980 are given respectively in Tables 2 and 3, and plotted on the left and right columns in Fig. 4.

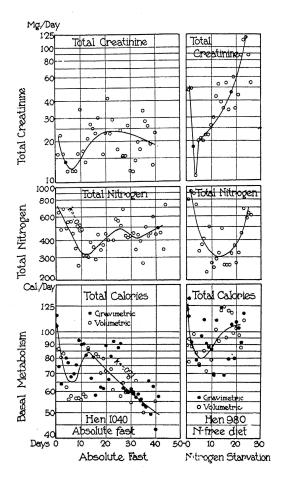
TABLE 3.—METABOLISM DATA FOR HEN NO. 980								
Fast Days	Body Wt. Gms.	Cals./day Volumetr. Method	Cals./day Gravimetr. Method	Ratio Vol. to Gravim.	Total N Excret. mg./day	Total Creatinine mg./day	Cals. From Prot.	Ratio Cals from Prot to Toral Cals. %
Normal Normal Normal 1 2 3 4 5 6 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23	1800 1827	127.2 131.4 135.4 121.3 85.3 98.4 88.8 61.9 85.4 71.2 69.6 102.5 120.7 120.0 117.6 99.2 103.2 110.2	155.2 114.18 104.8 104.8 104.3 91.6 (86.0) 75.5 96.5 110.8 90.9 87.5 86.3 110.7 (93.0) 79.5 103.0) 79.8 103.2 91.3	82.0 115.8 87.5 111.4 68.4 (114.8 100.4 101.0 91.5 101.0 91.5 92.6 (96.0) 98.1 180.9 150.9	801 926 892 728 327 372 407 232 504 269 250 486 259 258 259 259 259 259 259 269 269 270 323 485 684 684 684 687 610	48.0 49.0 17.0 11.0 20.0 22.0 22.0 22.0 26.0 30.0 43.0 35.0 46.0 35.0 44.0 46.0 35.0 44.0 46.0 35.0	21.2 24.6 21.3 24.6 19.3 10.8 10.8 10.8 13.4 16.6 6.8 12.9 6.8 9.7 8.6 11.1 11.1 11.1 11.1 11.1 11.1 11.1	17.1 19.8 19.0 15.6 8.1 11.0 12.7 16.8 9.3 10.0 14.7 7.3 7.3 8.6 97.1 8.4 11.6 17.2 16.4 11.4 15.4

Table 3.—Metabolism Data for Hen No. 980

Total loss in live weight, 506 grams; percentage loss in live weight, 27.4%. Total heat production for volumetric method and gravimetric method is 2159 and 2187 Calories, respectively.

Nitrogen excreted, 8484 mg. (22 days); creatinine excreted, 1066 mg. (22 days).

There is much difference between the heat production on Hens 11 1040, and 980. While the heat production for Hen 11 (Fig. 2) declines continuously and uneventfully from the initial 125 to the final 35 Calories per day, the heat production of 1040 declines from an initial level of about 125 to about 65 Calories on about the 5th day. It then seems to rise to about 85 Calories by the 12th day, followed by a steady decline to about 50 Calories on the 40th day (as compared to about 42 Calories on the 40th day in Hen 11). Beginning with the 12th day, the slope of the curves is practically the same in Hens 11 and 1040—the declines



in both cases being of the order of 2% per day. The influence of "temperament" and "training" is best illustrated by the relatively good consistency and regularity of distribution of the data points for Hen 11 (Fig. 2), and the relative erratic distribution of the data points, and poor agreement between the results of the volumetric and gravimetric methods for hen 1040. The situation is still worse as regards the distribution of the data points for hen 980 which had access to the N-free, and evidently vitamin deficient, diet.

Fig. 4.—The energy and nitrogen metabolism of Hen 1040 (left column of curves) having access to water and sand, but no food; and Hen 980 (right column of curves) having access to the N-free diet. Note the, relatively, very erratic distribution of data for these "inexperienced" and "untrained" birds as compared to the, relatively, orderly and consistent distribution of data for Hen 11 (Fig. 2) which has been thoroughly habituated for metabolism experiments.

Table 4.—Composition of the Birds (White Rock Hens)

	(,
Chicken Number	11	1040	1287
Original Weight	18 4 0	1974	1814
Weight after fasting	690	776	Normal
Air-dry weight of chicken less feathers	173.2	263.8	652.22
Weight of feathers	120.5	104.2	73.8
Grams of Ether Extract in carcass	4.75	60.62	267.84
Grams of Ether Extract in feathers	.77	.94	.30
Grams of Nitrogen in Carcass	19.36	23.22	46.22
Grams of Nitrogen in Feathers	17.69	15.84	10.70
Per cent Ether Extract		7.93	14.77
Per cent Nitrogen	5.37	5.05	3.14
Total Protein, Gms	231.6	244.1	355.8
Nitrogen at beginning of fast	40.73	40.50	46.22
Percentage loss of nitrogen	52%	43%	
Percentage loss in body weight	62%	60%	- '

Bird No	11	1040	1287
Original Weight* Final Weight Feathers Digestive tract after opening and washing Pancreas Reproductive system, including ova Heart, including pericardium Liver and gall bladder Spleen Kidneys Respiratory system, including trachea Thyroids Thymus	1.0 3.8 10.8 15.8 0.2 4.5 8.0 0.105 0.120	1974 776 104.2 49.1 0.67 2.5 6.3 23.0 0.25 8.8 5.6 0.165 0.100	Normal Control 1814 1814 73.8 (moulting) 136.2 3.8 49.5 15.5 53.2 2.9 16.8 22.5 0.230 0.075 0.60

TABLE 5.—WEIGHTS OF ORGANS**

V. PUBLISHED DATA

It now seems desirable to examine the literature on long fasts of warm-blooded animals in some detail in order to compare our results with those found by others. We shall first consider studies on dogs.

1. Dogs.—Perhaps the best studies on the energy metabolism during complete fast leading to a fatal issue are due to Awrorow on the four dogs already mentioned. We have accordingly chosen for this work for analysis and for comparison with our data on the hens. In this connection, we wish to express our grateful appreciation to Miss E. A. Wilson, Secretary to Dr. Benedict, Carnegie Nutrition Laboratory, for her kindness in making available for this purpose Awrorow's dissertation.

We have plotted Awrorow's energy metabolism data in Fig. 5. The four dogs are represented from left to right in the order in which the data were reported by Awrorow. The columns, from bottom up, represent respectively total Calories per day, Calories per square meter per day, Calories per kilo per day, all against time; and finally on top, Calories per kilo per day plotted against body weight.

The curves in Fig. 5 correspond to curves in the left column of charts in Fig. 2, on our Hen 11.

Fig. 5 shows that there are enormous differences with regard to the survival period of the four dogs. Awrorow remarks on it, and explains it to be due to two factors, namely relative stores of fat in the body, and temperament of the animal. Dog 1, having the shortest survival period, was the leanest of the four, and also the most restless, the most nervous and unhappy. On the other hand, Dog 4 was the fattest and Awrorow writes very touchingly on the quiet stoicism of dogs 3 and 4. He speaks of age being another factor of possible importance. Dog 1

^{*}All weights in grams.
**Dissections by Mr. Harold C. McDougle.

appeared to be the youngest of the four, which may have contributed to his early death.

The second fact that strikes us as important is the slope of the curve when total metabolism per day is plotted against time. Dog 1, the shortest lived, shows a curve which is about twice as steep as the curves of Dogs 2 and 3. This means that the percentage decline in energy metabolism was twice as rapid for Dog 1 than for 2 or 3; its vitality (assuming metabolism to be an index of vitality) was declining twice as rapidly.

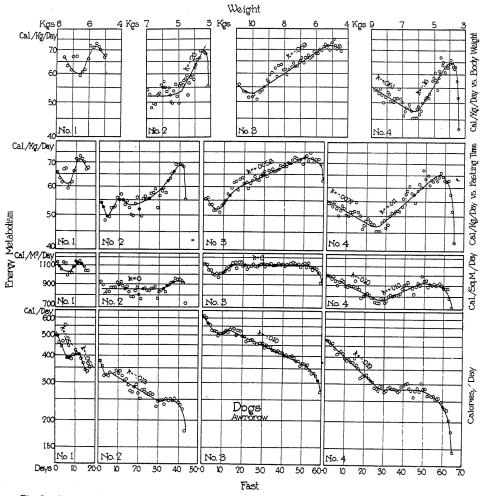


Fig. 5.—A comparison of the time curves of energy metabolism during complete fast, terminating in death, of four dogs. The charts, plotted from data by Awrorow, includes his dogs 1, 2, 3, and 4 as indicated on the charts. Note the individual differences in the survival periods of the dogs, and the shape of their time curves of energy metabolism. The uppermost four curves represent metabolism plotted against time of absolute fasting.

In the dog as well as in the chicken, we find an initial decline in metabolism per unit weight, presumably an expression of more economical use by the organism of its resources, followed by a rise. All the four dogs show this change in the per unit weight direction of the slope, but there is an enormous variation with regard to the time of the change. The rising phase in the time curve of fasting is probably associated with a relative increase in what Benedict calls "protoplasmic mass", or what Le Breton and Schaeffer call "masse protoplasmique active". following remarks by Awrorow are appropriate and enlightening in this connection: "We must not think that in the processes of the exchange of substances, the surface of the animal plays the exceptional role and thus entirely overshadows by itself the significance of the most vital elements—the tissues. Undoubtedly, the surface of the animal has an influence on the intensity of the oxidizing processes in the organism, since, first of all, the animal's heat expenditures depend upon the size of the surface; but this significance limits itself to the physical side of the matter. The metamorphosis in the animal organism excepting some exterior influences, depends upon interior causes, upon the quantities of living elements as well as on their natural intensity of vital functions, which causes a corresponding rise or fall of the oxidizing processes." The greater use of protein for energy purposes with the advance of the period of fasting should be mentioned as another very important factor contributing to the increasing metabolism per unit weight.

Fig. 6 presents the course of nitrogen excretion by Awrorow's dogs; also by Howe's dog "Oscar" during his famous 117-day fast. Oscar's total creatinine excretion is also given. The upper half of the chart represents the daily nitrogen and creatinine excretion per kilo of live weight, while the lower half of the chart represents the total excretion of these substances per day. The shapes of the time curves of the nitrogen excretion in Awrorow's dogs are very similar to the shapes of the time curve of energy metabolism. The individual variations in this respect are enormous, not only with regards to the absolute excretion, but also with regards to the shape of the curves. An interesting fact in this connection is that the nitrogen excretion per kilo body weight declines for Howe's dog during the first 30 days, while it increases in Awrorow's dogs. Howe's Scotch Collie was very economical with his resources as compared to Awrorow's Russian subjects. The contrast is astounding.

2. Humans.—As regards investigations on fasting humans, the best one is no doubt due to F. G. Benedict on Subject L. who fasted 31 days, losing during this period 19% of his body weight. This, of course, did not lead to a fatal issue so that these data are not comparable to our data on the fowls, or to Awrorow's data on dogs.

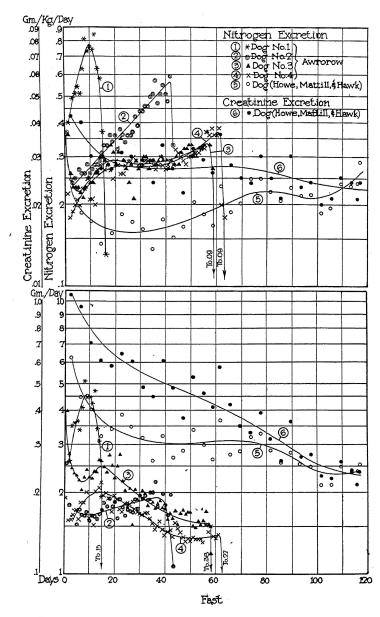


Fig. 6.—A comparison of the time curves of nitrogen excretion of Awrorow's dogs, and Howe's dog. The upper curves represent nitrogen and creatinine excretion per kilo live weight. The lower curves represent nitrogen and creatinine excretion per day.

Known fasts on humans which terminated in death, on the other hand, were not under scientific control or observation. Nevertheless, it is of interest to note a few such cases as indications of the possible survival period of humans during starvation.

The most widely known case of deliberate starvation was undertaken in 1919 by Terence MacSwiney, a former Lord Mayor of Cork, Ireland, in the interest of the Sinn Fein cause. This hunger strike was carried out while MacSwiney was in a London jail. He swooned on the 75th day when he was forcibly fed. This is of interest from the present point of view in indicating the time an adult human can survive under perhaps more or less favorable environmental conditions.

Less well-known political cases of hunger strikes (also in jails) are of Jatindranath Das, arrested in 1929 in the Lahore conspiracy, dying at the end of 61 days; Taha Hussein, after his attempted assassination of Egyptian Prime Minister Sidki Pasha, dying after 50 days.

It thus appears that the survival period of normal adult man is of the order of two to three months, and that even the longest recorded laboratory fast on man (Succi, 40 days) reached, perhaps, only half or even one-third of the normal survival period under favorable conditions, and therefore not comparable with our fasting data, or those of Awrorow which lead to a fatal issue under favorable environmental conditions.

A comparative graphic analysis of the fasting data on a man will nevertheless be of interest and so we have plotted in Fig. 7, the data on Benedict's Subject L.

As in the preceding charts, the data are plotted on arithlog paper, in this way obtaining perfectly comparable curves, regardless of the differences in the absolute units employed.

Fig. 7 shows that the basal metabolism, after a slight initial rise, declines at a nearly constant percentage rate (1.4 to 2% depending on the units of reference) until about the 15th day of fast. The metabolism is a nearly constant minimum (1100 Calories per day, 650 Calories per square meter per day, 21.5 Calories per kilo per day) between 15 and 25 days; then it slowly arises to the end. The nitrogen and creatinine excretion also show a pause of minimum excretion between 20 and 25 days, and the decline in the creatinine excretion with increase in the period of fast follows the same slope as the decline in energy metabolism (1.5 to 2.2% per day). The initial steep rise in the nitrogen and creatinine excretion does not have its counterpart in the energy metabolism curve.

The time curves of "basal" metabolism with the advance of the fasting period in humans (Fig. 7) show the same shapes and even the same slopes (about 2% per day of decline) as the curves of our hen 11

(Fig. 2); they are also somewhat similar to the curves of Awrorow's dog No. 4 (Fig. 5), that is, after taking into consideration the fact that the human curves extend to, possibly, only half of the period of survival.

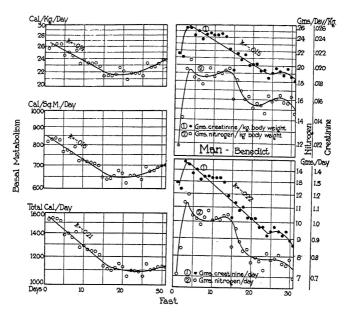


Fig. 7.—The course of energy and nitrogen metabolism with the advance of the period of fasting in a human (Benedict's fasting man L.). The minimum energy metabolism (on any basis) is reached between 20 and 25 days of the fast when the basal metabolism is about 650 Calories per square meter, or 21.5 Calories per kilo. This time also seems to indicate a minimum in the nitrogen and creatinine curves. What is the significance of the rise in nitrogen excretion during the first four days? Note that the total creatinine and energy metabolism curves have slopes (decline in metabolism) of 1.4 to 0.2 % per day.

As regards the time curves of nitrogen and creatinine excretion, the situation for humus (Fig. 7) is quite different from that found for Hen 11 (Fig. 2). The time curve for humans declines following the initial rise, while in the case of the hen it rises continuously almost to the end. It appears that the fowl can dispense with much more of its protein elements, or at least it uses, proportionately, much more of its nitrogenous substances than the human or dog (Fig. 6). This fact can also be demonstrated by comparing the percentages of protein used for energy needs in three species as illustrated in Fig. 8. Hen 11 begins by deriving only 6% of energy from protein. As the fast progresses, the percentage of protein used for energy steadily increases (at the rate of about 5% per day) to a maximum of 51%! Hen 1040 does not go up so high, still its proportion of energy derived from protein is higher than of the mammals shown by the curves in the lower half of the chart.

A closely related problem concerns the ratios of energy metabolism to nitrogen excretion and to creatinine excretion in the several species under discussion. These ratios are shown graphically in Fig. 9.

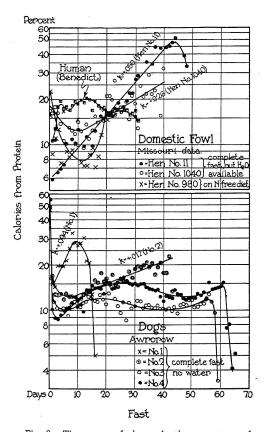


Fig. 8.—The course of change in the percentage of protein used for energy metabolism with the advance in the period of fasting. The upper half of the chart represents our hens; the lower half represents the dogs of Awrorow (Awrorow's dogs received no water, while our hens had access to water). The Calories derived from protein were computed by multiplying grams of urinary nitrogen by 26.51 (see Lusk, 4th edition, p. 68).

The upper left chart shows the changing ratios of heat production, Q, to nitrogen excretion, N; and to total creatinine excretion, Cr, for Hen 11. This ratio is seen to decline at an almost constant rate of 4.8 per cent per day. The other curves in Fig. 9 represent the ratios for humans and dogs.

It thus appears that energy metabolism is not proportional to total creatinine or total nitrogen excretion. In the fowl, those ratios (Q/N. or Q/Cr.) decline throughout the whole period of fasting; in humans

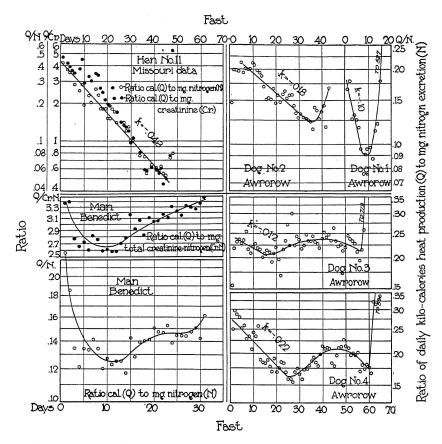


Fig. 9.—The course of change in the ratios of heat production, Q, to excretion of nitrogen, N, and total Creatinine, Cr.

and dogs, they decline in the initial stages of fasting followed by a more gradual rise for the later stages of fasting. The minimum for those ratios occur very early in man (about 10 days), and rather later in dogs. How should one explain the fact that these ratios continue an unbroken decline in the fowl, while in the other species the initial decline is followed by a rise? And how should one explain the individual differences in the curves for the dogs?

Finally, Fig. 10 is presented, indicating the course of decline in live weight with the advance of the period of fasting. In nearly all cases, there is an initial sharp decline of about 5 days duration, followed by a more gradual decline during the remainder of the period. In several cases, the decline becomes sharp again in the very last stage of the fast.

The data as plotted on an arithlog grid indicate that during each of the three periods (initial relatively steep decline, medium decline,

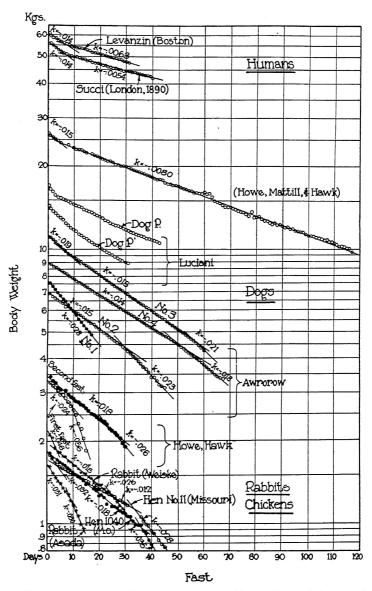


Fig. 10.—The course of decline in body weight with the advance of the stage of fasting as plotted on an arithlog grid. The numerical values of k when mu.tiplied by 100 indicate the percentage decline per day. Note that during the second fast of Howe's smaller dog the decline in body weight is much less rapid than during the first fast, the animals having been habituated to this experience.

final steep decline) the declines occur at constant percentage rates; and that the smaller the animal, the greater the percentage decline in weight. Thus Howe's large dog loses weight at the rate of 0.80 per cent per day, while Howe's smaller dog declines in weight (during the second fast) at the rate of 1.8 per cent per day. The loss in the humans, Levanzin and Succi, is between 0.5 and 0.6 per cent per day—that is, after the initial sharp decline which proceeds at 1.4 per cent per day. The percentage rate of loss in body weight in our hens is 1.2 to 1.8 per cent per day, and is of the same order as in Awrorow's dogs or Howe's smaller dog, or Weiske's rabbit. Asada's small rabbit, which was not given water during the fast, lost weight more rapidly.

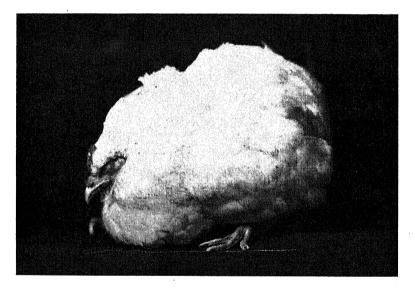


Fig. 11.—Hen No. 11 on the day preceding her death

SUMMARY AND CONCLUSIONS

1. One White Leghorn hen, habituated to laboratory life, survived 49 days without food (water accessible), losing during this time over 61% of her body weight. Her energy metabolism was measured daily by the Haldane gravimetric method (confinement period of two hours), and also by a volumetric method (confinement period 30 to 60 minutes). While there were considerable differences in the results on given days, the differences appeared to be due to differences in the relative degrees of restlessness of the subject rather than to differences of methods in measuring metabolism. If other conditions are the same, there is good agreement between the results of the gravimetric and volumetric methods

referred to in the text. Successive measurements agree to within at least 7% of each other. The volumetric method of measuring metabolism appears to be as reliable as the Haldane gravimetric method provided that the temperature of the system remains constant to within 1°C.

Another hen (White Rock), not habituated to laboratory life, was subjected to similar conditions of fast. The metabolic values of this bird was much less consistent, in fact often quite erratic, thus indicating that training and experience are important factors in the success of measuring metabolism even by the chamber method. A third hen, confined to a nitrogen-free diet, survived less than half of the time of the birds not given any food, indicating that no food is often better than a poor diet; also indicating that the domestic fowl is much more sensitive to polyneuritis when fed an N-free diet, than when fasted. Rats survived on this same N-free diet over 3 months.

Although several investigators have sought a connection between vitamin B deficiency and carbohydrate metabolism no direct comparison seems to have been made between animals completely fasting and those suffering from specific nitrogen inanition. However, it has been suggested that voluntary fasting of animals on vitamin B deficient diets is due to an attempt of the organism to liberate by tissue-wasting some of the body stores of viramin B. A recent review of the subject is given by Sherman and Smith.

- 2. The excretion of total creatinine and total nitrogen followed nearly the same course throughout the entire fast in the domestic fowl.
- 3. While the energy metabolism declines more or less steadily throughout the fast, the nitrogen and total creatinine excretion increase with the advance of the stage of fasting. Our data on the hens differ in this respect from published data on dogs and humans.
- 4. Detailed comparisons are presented between the data we obtained on our domestic fowl with published data on fasting dogs and a human. The shape of the time curves of energy metabolism of our hens is quite similar to the curves of fasting dogs and of the human. The total metabolism per day tends to decline between the rates of 1 and 2% per day. As regards the metabolism per square meter, this declines in all cases in the initial stages of the fast, then tends to remain constant, or even rises somewhat. The minimum value is of the order of 450 Calories per square meter per day in the hen (reached by the 20th day of fasting); 650 Calories per square meter per day in the human (reached by the 17th day of fast); 800 Calories per square meter per day in dogs. The differences between the absolute values of metabolism per square meter for these species are perhaps without significance depending on the surface-area formulae employed.

The minima for metabolism per unit weight are about 35 Calories per kilo or 400 Calories per square meter per day for the fowl (reached between the 10th and 20th day of fast); 21 Calories per kilo or 625 Calories per square meter per day for the human (reached by the 15th day); and from 45 to 60 Calories per kilo per day in the dog, depending on the size and temperament of the animal.

There are immense individual variations in the intensity of metabolism, shape of the time curves, and survival periods. Other conditions being the same, these variations are believed to be due to "temperamental" differences in the individuals, including the factor of training.

As regards the course of nitrogen and total creatinine excretion, the differences between our hens and the published data on dogs and the human are very considerable. The nitrogen and creatinine excretion by our hens increase quite steeply from the 15th day to about 35 or 40 days, when 90 milligrams of total creatinine and 900 milligrams of total nitrogen are excreted per kilo per day. In the human, following an initial 4-day rise, the excretion of these substances decrease. In the case of dogs, in some individuals the nitrogen rises steadily as in the fowl; in others, the rise is succeeded in the middle of the fast by a rapid decline; in still others, the level of nitrogen excretion remains practically constant after an initial 10-day rise (in some cases a decline) in the N-excretion. One important conclusion is that there are tremendous individual variations in this respect, and that a good deal remains to be learned about the mechanisms of these variations. It is certain that one can not generalize on the basis of results obtained on one animal regardless of the technique employed.

5. The enormous rise in nitrogen excretion in the fowl as compared to that in other species is also shown by the fact that the energy derived in the fowl increases from an initial value of 6 to a final value of 50 per cent of the total energy; while in dogs, the rise is from 9 to a maximum of 23 per cent of the total energy. In one dog the maximum on the 58th day of fasting was only about 13 per cent of the total energy.

This is also illustrated by the time curves of the ratios of Calories to total creatinine or Calories to nitrogen excretion. These decline in the hen with the advance of the stage of fasting at the constant rate of 4.8 per cent per day. The Calories per milligram total creatinine excretion fall from an initial value of 5 to a final value of 0.5; the Calories per milligram nitrogen excretion fall from an initial value of 0.42 to a final value of 0.052. In the human, on the other hand, the Calories per milligram nitrogen fall from 0.22 to about 0.13 by the 12th day, then rise again to about 0.16 on the 31st day. In dogs, likewise, the ratios first decline then rise, but with many individual variations in this respect.

The great individual and species variations make the situation too confusing for further interpretation or generalization at this time. It appears that it is not the changes in percentage of creatinine or nitrogen in the body that cause these changes in excretion of these substances with the advance in the stage of fasting; for the percentages of these substances in the bodies of rats remain constant throughout the entire period of fasting if expressed as percentage of fat-free and ash-free dry tissues. This has been demonstrated by Terroine and Chanutin.

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ADDENDA:—Since the above was written Benedict, Horst, and Mendel (J. Nutrition, 1932, 5, 571), reported energy metabolism, and live weight data on a 56- and on a 38-day fast on two rats of extraordinary size (797 and 706 grams). The shapes of the time curves for live weight and metabolism of these rats are similar to our time curves for the domestic fowl (Fig. 2). In working over their data we found that the decline in body weight between 5 and 43 days is of the order of 1.2 per cent per day; following this time, the decline was greater, somewhat irregular, and of the order of 1.8 per cent per day. The metabolism per kilo up to 15 days, declined at the rate of 1.5 per cent per day for the larger rat, and 1.0 per cent for the smaller rat. This is followed by an irregular period, ending with an increased rate of about 1.8 per cent per day. The situation is similar when expressed in terms of Calories per square meter. The minima are of the order of 400 Calories per square meter per day (or about 45 Calories per kilo) for the larger rat, and about 530 Calories per square meter (or about 60 Calories per kilo) for the smaller rat. The minima occurred in the region of 25 days of fast. It may be recalled that in the case of our Hen No. 11, we found on the 20th day a minimum of the order of 400 Calories per square meter per day, or 35 Calories per kilo per day, and the body weight declined at the rate of 1.2 per cent per day. It is, of course, very surprising that our data on the domestic fowl should be so close to that of the rat.

APPENDIX

Notes on Two-Months Fasts in Swine

S. R. Johnson

While fasting the 3 chickens described in the text, it was thought desirable to try similar fasts on swine. Two sows, Nos. 37 and 38, (born Aug. 8, 1929), were available for this purpose. They were exceedingly fat (weighing respectively 280 and 264 kilos) and apparently not in good health. The fasts and energy metabolism measurements (by the oxygen consumption method described on pp. 6 to 17, Missouri Res. Bull. 143) were begun early in July, 1932, and continued until they died about 2 months later. Their death was not, however, due to inanition as such, as the carcasses of these animals were hardly inferior to the average market hogs with respect to their amounts of fat contained. The animals appeared to have suffered from some deficiency ailment as evidenced by their high rectal temperatures, extreme leg weakness, frequent passing of blood from the rectum and the extensive hemorrhages in the digestive tract found on autopsy. They also suffered from hot weather, as the barn temperature frequently mounted to 35° C., and it rarely, even at night, fell below 25° C.

These considerations make it difficult to interpret the results. The data, shown in Fig. 12, are therefore presented without interpretations as regards the influence of fasting in *normal* swine on metabolism.

The bottom-left curves (Fig. 12) represent the decline in live weight of the animals. The decline is very slow (about 0.37 per cent per day).

The other curves in the left column represent the nitrogen and creatnine excreton of sow 38. The urinary nitrogen is seen to decine from about 40 to about 23 mg. per kilo of live weight. The latter value is rather low when compared to the values in Mitchell's tabulations. The irregularities in nitrogen excretion are probably due to the fact that the animals were allowed to urinate naturally, and the amount of urine in the bladder undoubtedly varied from day to day. The creatinine coefficient remained nearly constant, and it is of the order of about 22 mg. per kilo live weight—which is near the value found in humans.

The energy metabolism for sows 38 and 37 are represented respectively, in the center and right columns of Fig. 12. The upper curves represent the rectal temperatures of these animals, the rises of which may explain the rises in energy metabolism (instead of the expected decline as found for the other species discussed in this bulletin).

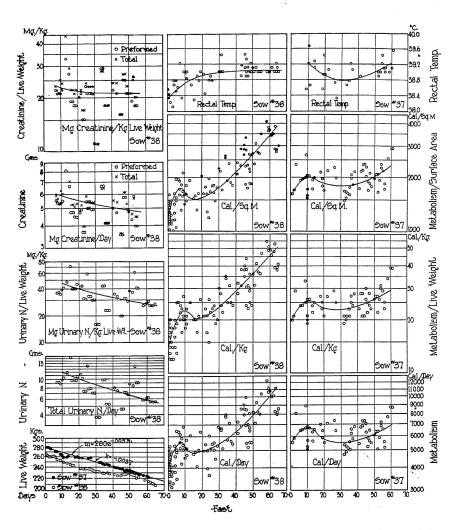


Fig. 12. The course of change of body weight, urinary nitrogen excretion, creatinine excretion, energy metabolism, and rectal temperatures of two 3-year-old very fat sows.