Issued February 15, 1912.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF ANIMAL INDUSTRY.—BULLETIN 143.
A. D. MELVIN, CHIEF OF BUREAU.

THE MAINTENANCE RATIONS OF FARM ANIMALS.

BY

HENRY PRENTISS ARMSBY, PH. D., LL. D.,
Director of the Institute of Animal Nutrition of The Pennsylvania State College; Expert in Animal Nutrition, Bureau of Animal Industry.

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Animal Industry,
Washington, D. C., August 12, 1911.

Sir: I have the honor to transmit herewith, and to recommend for publication in the bulletin series of this bureau, a manuscript entitled "The Maintenance Rations of Farm Animals," by Dr. Henry Prentiss Armsby, who has charge of the cooperative work in animal nutrition between this bureau and the Institute of Animal Nutrition of The Pennsylvania State College. The paper is based not only on Dr. Armsby's own work, but on that of other investigators as well, and is believed to cover the subject thoroughly.

Respectfully,

A. D. Melvin,
Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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ILLUSTRATION.

THE MAINTENANCE RATIONS OF FARM ANIMALS.

INTRODUCTION.

Feed is supplied to farm animals in order that they may either yield products useful to man as materials for human food and clothing or serve him by the performance of mechanical work. But as a factory must first be supplied with enough power to keep in motion the shafting, belting, and other machinery before any product can be turned out, so the animal mechanism must be provided with sufficient feed to maintain the processes essential to life before any continued production is possible. The amount of feed required for this purpose is called the maintenance ration of the particular animal. It is the quantity of feed necessary simply to support the animal when doing no work and yielding no material product. If an animal receiving exactly a maintenance ration were subjected to a so-called balance experiment, there would be found an exact equality between income and outgo of ash, nitrogen, carbon, hydrogen, and energy, showing that the body was neither gaining nor losing protein, fat, carbohydrates, or ash.

The word "maintenance" is sometimes used popularly in another sense to signify the total amount of feed required, for example, by a horse in order to perform his daily work or by a calf in order to make a normal growth. It is important to grasp the idea that, in its technical sense, the maintenance requirement means the minimum required simply to sustain life. The feed of the horse or calf would, from this point of view, be regarded as consisting of two portions; one of these is the maintenance ration, which if fed by itself would just support the horse at rest or the calf without growth, and the other the productive portion of the ration by means of which work is done or growth made. To recur to the illustration of the factory, the maintenance ration keeps the empty machinery running, while the additional feed furnishes the power necessary to turn out the product.

It might seem at first thought that not much importance attaches to a study of the maintenance ration. The animal kept on such a ration yields no direct economic return and hence simple maintenance feeding should be avoided, so far as practicable, and when it appears desirable to practice it the observation of the skilled stockman, especially if supplemented by occasional weighings, will usually suffice to determine whether or not the end is being attained. Nevertheless, the subject has significance for practice as well as for science. A very considerable fraction of the feed actually consumed by farm animals—on the average probably fully one-half—is applied simply to maintenance. But if half of the farmer's feed bill is expended for maintenance, it is clearly important for him to know something of the laws of maintenance—how its requirements vary as between different animals, how they are affected by the conditions under which animals are kept, how different feeding stuffs compare in value, etc.—as well as to understand the principles governing the production of meat, milk, or work from the other half of his feed.

Physiologically, too, the maintenance requirement represents the demand of the basal life processes. The prime necessity of the organism is to maintain itself. It must live before it can grow or propagate its kind, and in the phenomena of maintenance the fundamental processes of nutrition may be studied uncomplicated by the demands of growth, fattening, or reproduction.

THE FASTING KATABOLISM.[1]

Unlike the operations of a factory, which cease when the power is shut off, the activities of the animal do not stop when food is withdrawn, but continue for a variable length of time at the expense of the materials of the body. It is as if the materials of the factory itself were being cut up and used for fuel under the boilers. Men have fasted voluntarily for 30 days or more without obvious permanent ill effects, and there are records of dogs having survived fasting periods of from 90 to 100 or more days. In the fasting animal at rest the vital activities are reduced, as it were, to their simplest terms, practically only those functions being active which are essential to continued life. The following approximate estimate by Zuntz of the factors of the katabolism of a fasting man may serve to give a general idea of their nature and relative importance. The figures show the oxygen consumption per minute of the various tissues and its percentage distribution:

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[1] For references to the literature of the fasting katabolism compare:

Magnus Levy. Von Noorden's Pathologie des Stoffwechsels, 2d ed., I, 222–225 and 310–315.

Tigerstedt. Nagel's Handbuch der Physiologie des Menschen, I, 375–391.

Lusk. The Science of Nutrition. 2d ed., 54–85.

Benedict. Metabolism in Inanition. Carnegie Institution of Washington, Publication No. 77, II, 361–364.

Armsby. Principles of Animal Nutrition, 3d ed., 80–92 and 340–347.

Consumption of oxygen in fasting man weighing 70 kilograms—Zuntz.

	Cubic centimeters per minute.		Percentage.	
Circulation and respiration		30.0		12.45
Voluntary muscles		112.0		46.49
Glands and other organs:				
Liver	45.0		18.68	
Small intestine	25.1		10.42	
Kidneys	10.5		4.36	
Pancreas	9.3		3.86	
Large intestine	7.0		2.91	
Salivary glands	2.0		.83	
		98.9		41.06
Total		240.9		100.00

According to the foregoing table nearly 60 per cent of the metabolism of a fasting man is due to the work of the muscles, including that of respiration and circulation as well as the limited activity of the voluntary muscles, while somewhat over 40 per cent is due to the internal organs. No equally complete data are available for farm animals, but the supposition seems justified that their metabolism in its main features is not greatly unlike that of man. It may be noted that Zuntz and Hagemann found the energy expended in respiration and circulation by the horse in a state of rest to be, respectively, 4.7 and 5.01 per cent of the total metabolism. The sum of these—9.71 per cent—is approximately comparable with the corresponding figure for man.

PURPOSE OF THE FASTING KATABOLISM.

The animal body is primarily a transformer of energy. From the biochemical standpoint the essential phenomenon of physical life is the transformation of chemical into kinetic energy which accompanies the breaking down of more or less complex molecules into simpler ones, and all vital activities are essentially manifestations of energy. In the fasting state this energy is derived from the store of chemical energy contained in the materials of the body itself. The very act of living, in the foregoing view of it, is synonymous with the expenditure by the organism of its stored-up capital of energy. The prime and dominating purpose of the fasting katabolism, therefore, is to supply energy for the life actions.

But since the necessary activities of the fasting organism are carried on by means of energy derived from the katabolism of materials contained in the tissues, the body's store of matter and of energy is being constantly depleted. To prevent or replace this loss will require a corresponding supply of available material and energy in the feed. A knowledge of the kind and quantity of material katabolized during fasting and of the amount of energy liberated, therefore, is obviously the first step toward ascertaining the supply necessary in the feed.

THE MATERIAL KATABOLIZED.

Ash.—The fasting organism suffers a continual loss of the so-called ash ingredients of its tissues, including both the sulphur and phosphorus of its proteins and the more distinctly "mineral" elements, such as sodium, potassium, calcium, magnesium, chlorin, etc. These elements are just as essential to the existence of the animal as are the carbon, nitrogen, hydrogen, and oxygen of the so-called "organic" compounds.

The study of this branch of the subject, however, has hardly progressed far enough as yet to permit a definite formulation of the ash requirements of domestic animals. The present paper, therefore, will be confined to a discussion of the maintenance requirements in the more limited and customary sense, including only those substances whose function it is wholly or in part to serve as sources of energy.

Fat.—It is a familiar conception that fat formation is the body's method of disposing of surplus feed, and that the body fat is a store of reserve fuel material. The converse of this fact is equally familiar. The fasting or insufficiently fed animal loses fat and may reach a stage of extreme emaciation before the active tissues fail to perform their duties. Obviously, the fasting animal lives very largely upon its reserve fat. These conclusions from common observation have been fully confirmed by comparative analyses of the carcasses of well-fed and of fasted animals as well as by the results of balance experiments in which the exact nature of the outgo from the body has been determined.

Carbohydrates.—In addition to fat, the body stores up more or less nonnitrogenous matter in the form of glycogen in the liver and muscles. During the first few days of fasting this store of carbohydrates is also drawn upon, as is indicated by the fact that the respiratory quotient tends to approach unity, while later the amount katabolized becomes very small. This is well illustrated by Benedict's[1] experiments upon fasting men. The average results of a number of experiments in which men fasted for from two to seven consecutive days were as follows:

Glycogen katabolized by fasting men—Benedict.

Day.	Number of subjects.	Glycogen katabolized.	
		Total.	Per kilogram of body weight.
		Grams.	*Grams.*
First day	14	110.0	1.69
Second day	[2] 13	40.3	.62
Third day	6	21.8	.36
Fourth day	5	23.3	.40
Fifth day	[2] 1	8.2	.14
Sixth day	1	21.7	.38
Seventh day	1	18.7	.33

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[1] The Influence of Inanition on Metabolism. Carnegie Institution of Washington, D. C., 1907, p. 464.

[2] Another subject showed a slight gain of glycogen.

Protein.—Balance experiments, however, while confirming the conclusion that the loss of tissue in fasting usually consists chiefly of fat together with some carbohydrates, show that there is also a continual breaking down of body protein and a corresponding excretion of urinary nitrogen. While the energy supply of the fasting animal is chiefly derived from the breaking down of nonnitrogenous material, the functional activity of the tissues necessarily involves the katabolism of a certain amount of protein.

RATIO OF PROTEIN TO TOTAL KATABOLISM.

Qualitatively, then, the katabolism of the fasting animal is substantially a katabolism of fat and of protein, and it becomes of interest to consider the quantitative relations between the two. Such a comparison is best made on the basis of the amounts of energy liberated in the body in the katabolism of protein and of fat respectively. This aspect of the subject has been treated especially in an article by E. Voit [2] in which the results of a considerable number of fasting experiments are compiled and discussed. While some of Voit's computations are based on estimates, they are sufficiently accurate to outline definitely the main features of the fasting katabolism. Including only experiments on animals well nourished at the beginning, he obtained the following averages for the percentage of the total energy liberated which was supplied by the katabolism of protein in the case of a number of different species. The results of the first day or two of fasting are not included in the averages.

Proportion of energy derived from protein in fasting—E. Voit.

Kind of animal.	Live weight.	Protein katabolism in per cent of total katabolism.
	Kilos.	*Per cent.*
Swine	115.0	7.3
Man	63.7	15.6
Dog	28.6	13.2
	18.7	10.7
	7.2	13.5
Rabbit	2.7	16.5
Guinea pig	.6	10.8
Goose	3.3	7.4
Hen	2.1	10.0

While both the total and protein katabolism naturally showed a wide range as to absolute amount, whether per head or per unit of live weight, the ratio of protein to total katabolism proved notably uniform with only two exceptions. The experiments upon dogs, 27 in number, included in the foregoing table furnished the basis for the following comparison, showing that in 74 per cent of the cases the ratio ranged from 10 to 17 per cent.

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[1] Zeitschrift für Biologie, vol. 41, p. 167.

Protein katabolism of dog in per cent of total katabolism.

	Number of cases.	
	Absolute.	Per cent.
Less than 10 per cent	4	14.8
10 to 14 per cent	15	55.6
14 to 17 per cent	5	18.5
More than 17 per cent	3	11.1
	27	100.0

It may be accepted as established, then, that in what may be spoken of as the normal fasting animal, in which the influence of the previous feeding has disappeared and in which, on the other hand, the fat reserve has not been exhausted, the protein katabolism constitutes a fairly small percentage of the total katabolism, both being expressed in terms of energy.

INFLUENCE OF BODY FAT.

It is clear, however, from the foregoing figures that the ratio of protein to total katabolism may vary considerably. The most important factor in this variation has been found to be the relative amount of fat contained in the body. So long as fuel material in the form of body fat is readily available, the amount of protein katabolized remains small. Usually, however, the store of fat in the body is less than that of protein, while in fasting its exhaustion is relatively more rapid. There comes a time, therefore, when the supply of non-nitrogenous material to the tissues begins to flag. When this happens, the protein katabolism begins to increase—that is, when the supply of reserve fuel material runs low the organism begins to use the protein of its own tissues as a source of energy, and E. Voit[1] shows that this occurs whenever the ratio of fat to protein remaining in the body falls below a certain limit. If the animal was originally well fed, this rise in the protein katabolism occurs only shortly before death, from which fact it has received the name of the premortal rise. In the case of very fat animals this point may never be reached, while, on the other hand, in a lean animal the protein katabolism may increase steadily from the very beginning of the fasting. The following three experiments upon a fat guinea pig, a moderately fat dog, and a lean rabbit, cited by Voit from Rubner's experiments, may serve to illustrate these three types of fasting katabolism:

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[1] Loc. cit., p. 502.

Proportion of energy derived from protein—Rubner.

Guinea pig.		Dog.		Rabbit.	
Day of fasting.	Protein katabolism in per cent of total katabolism.	Day of fasting.	Protein katabolism in per cent of total katabolism.	Day of fasting.	Protein katabolism in per cent of total katabolism.
	Per cent.		*Per cent.*		*Per cent.*
2	10.4	2–4	16.3	3	16.5
3	11.1	10–11	13.1	5–7	23.6
4	11.0	12	15.5	9–12	26.5
5	11.9	13	17.4	13–15	29.8
6	11.8	14	20.0	16	50.1
7	6.9			17–18	96.4
8	11.2				
9	10.9				

INFLUENCE OF SURPLUS PROTEIN.

On the other hand, as Pettenkofer and Voit long ago showed,[1] when an animal which has been previously receiving large amounts of protein is deprived of feed, the high protein katabolism which is observed during the first two or three days of fasting is accompanied by a relatively smaller katabolism of fat. Thus in an experiment with a dog, cited on a subsequent page (p. 74) to illustrate the initial fall of protein katabolism, respiration experiments were made on the second, fifth, and eighth days, with the following results:

Katabolism of fasting dog—Voit.

Day.	Urinary nitrogen.	Fat katabolized.	Protein katabolized in per cent of total katabolism.
	Grams.	*Grams.*	
Second day	11.6	86	26.2
Fifth day	5.7	103	12.7
Eighth day	4.7	99	11.1

Obviously we have here the reverse of what takes place in the later days of fasting, viz, a gradual substitution of fat for protein as the readily available supply of the latter in the body is reduced. Doubtless the effect would have been found to be still more marked on the first day of the fasting, when the protein katabolism was equivalent to 28.1 grams of nitrogen.

RELATIVE CONSTANCY OF ENERGY KATABOLISM.

The results which have just been considered regarding the nature of the material katabolized in fasting and the way in which fat,

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[1] Zeitschrift für Biologie, vol. 7, p. 369.

carbohydrates, and protein mutually replace each other as fuel material as one or the other is most available fully substantiate the assertion made on page 9 that the controlling factor in the katabolism of the fasting body is the demand for energy. As there stated, the body is essentially a converter of energy, and protein occupies a peculiar position in nutrition simply so far as it is a part of the necessary mechanism for this conversion. These facts can hardly have failed to suggest that the demand for energy must be relatively constant in the same individual, and that such is in fact the case has been demonstrated by a large number of experiments.

For example, in the experiment by Voit upon a dog, just cited, the energy of the protein and fat katabolized on the three days, as computed from the data for the urinary nitrogen and for the fat katabolism, was as shown in the following table, from which it appears that the total energy katabolized, especially when computed per kilogram of live weight, was approximately the same on the different days.

Constancy of katabolism of fasting dog—Voit.

Day.	Live weight.	Energy from protein.	Energy from fat.	Total energy.	Total energy per kilogram live weight.
	Kilos.	*Calories.*[1]	*Calories.*[1]	*Calories.*[1]	*Calories.*[1]
Second day	32.87	289.3	816.9	1,106.2	33.66
Fifth day	31.67	142.2	978.5	1,120.7	35.38
Eighth day	30.54	117.2	942.4	1,059.6	34.70

[1] Throughout this bulletin the word "calorie" signifies the large, or kilogram, calorie, unless the contrary is specifically stated.

The same constancy is illustrated by Rubner's experiments on a rabbit, a dog, and a guinea pig, whose relative protein katabolism was tabulated on page 13. The latter is repeated in the following table, together with the heat production as measured directly or the carbon dioxid excreted, which may be assumed to be an approximate measure of the energy katabolized. As the table shows, notwithstanding very considerable variations in the relative amount of protein katabolized, the total energy liberated in the body was relatively very constant.

Constancy of katabolism of fasting animals—Rubner.

Day of fasting.	Guinea pig.		Dog.		Rabbit.	
	Protein katabolism in per cent of total katabolism.	Heat production per kilogram.	Protein katabolism in per cent of total katabolism.	Carbon dioxid per kilogram.	Protein katabolism in per cent of total katabolism.	Carbon dioxid per kilogram.
		Calories.		*Grams.*		*Grams.*
First		149.9		20.70		
Second	10.4	162.6		17.83		
Third	11.1	156.5	16.3		16.5	
Fourth	11.0	140.5		17.99		
Fifth	11.9	137.3			23.6	17.26
Sixth	11.8	150.6				
Seventh	6.9	157.4				15.90
Eighth	11.2	155.6				
Ninth	10.9	162.6			26.5	15.90
Tenth			13.1	18.70		15.65
Eleventh				17.86		
Twelfth			15.5	16.13		17.18
Thirteenth			17.4	17.06	29.8	15.81
Fourteenth			20.0	16.12		15.95
Fifteenth						15.90
Sixteenth					50.1	
Seventeenth					96.4	
Eighteenth						

Benedict[1] has obtained like results for the heat production of man as measured directly by means of the respiration calorimeter. For example, in an experiment[2] covering seven days the following quantities of energy were katabolized daily.

Constancy of katabolism of fasting man—Benedict.

Day of fasting.	Energy from protein.	Energy from fat.	Energy from glycogen.	Total energy.	Energy per kilogram body weight.	Protein katabolism in per cent of total katabolism.
	Calories.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Per cent.*
First day	318	1,175	272	1,765	29.7	17.7
Second day	286	1,385	97	1,768	29.9	16.0
Third day	303	1,471	23	1,797	30.8	17.0
Fourth day	248	1,422	105	1,775	30.8	14.3
Fifth day	221	1,394	34	1,649	29.0	13.5
Sixth day	218	1,244	91	1,553	27.5	14.1
Seventh day	204	1,286	78	1,568	28.0	13.2

This constancy of the fasting katabolism evidently is in accord with the conception of it outlined on page 9 as the measure of the energy necessary to carry on the vital activities of the body. The functions of circulation, respiration, excretion, etc., must go on continually in a state of so-called rest, the muscular tonus must be maintained and divers minor muscular movements executed. In the aggregate all these result in the expenditure of a relatively uniform amount of energy from day to day. This energy in the

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[1] The Influence of Inanition on Metabolism. Carnegie Institution of Washington, 1907, Publication No. 77.

[2] Experiment No. 75 on S. A. B., pp. 188, 483, and 496.

fasting animal is supplied mainly by the katabolism of protein and fat. In the intermediate stages of fasting, as has been shown, the katabolism is largely that of fat, but the ratio between fat and protein katabolized may differ widely according to circumstances. In other words the protein requirement, or at least the amount of protein used, may vary, while the energy requirement remains nearly constant. The fasting organism requires a definite quantity of energy, but seems more or less indifferent as to its source.

THE ENERGY REQUIREMENT FOR MAINTENANCE.

In the fasting animal the store of potential energy in the body is diminished daily by the amount required to carry on the vital activities, this amount being, as just shown, relatively constant. In order to prevent such a loss and maintain the store of body energy, it is evident that a corresponding quantity of energy must be supplied in the feed and that a maintenance ration is one which supplies this requisite quantity.

REPLACEMENT OF NUTRIENTS.

For this purpose experiments have shown that the various digestible nutrients may replace each other or the ingredients of the body through a very wide range.

FEED FAT AND BODY FAT.

Fat fed to a previously fasting animal diminishes or suspends the loss of body fat. The following averages of Pettenkofer and Voit's experiments,[1] computed from Atwater and Langworthy's digest,[2] may serve to illustrate this substitution of feed fat for body fat:

Replacement of body fat by feed fat—Pettenkofer and Voit.

Food.	Number of experiments.	Gain or loss by body.	
		Nitrogen.	Fat.
		Grams.	*Grams.*
None	5	−6.64	− 97.76
100 grams fat	2	−4.90	− 16.25
350 grams fat	1	−7.70	+113.60

The smaller amount of fat not only diminished the protein katabolism but also largely reduced the loss of fat from the body. While the larger amount of fat showed a tendency to increase the protein katabolism, it not only suspended the loss of body fat but caused a storage of fat in the organism. Of course there is no means of distinguishing in such a case between feed fat and

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[1] Zeitschrift für Biologie, vol. 5, p. 370.

[2] U. S. Department of Agriculture, Office of Experiment Stations, Bulletin 45.

body fat, but it is most natural to suppose that the resorbed fat of the feed, being already in circulation in the body, is more easily accessible to the active cells than the stored-up fat of the adipose tissue and is therefore metabolized in preference to the latter.

CARBOHYDRATES AND BODY FAT.

Experiments precisely similar to those on fat just described show that carbohydrates may also diminish or suspend the loss of body fat. This may be illustrated by the results of three experiments upon a dog by Rubner.

Replacement of body fat by carbohydrates—Rubner.

Food.	Total nitrogen of excreta.	Total carbon of excreta.	Gain or loss of fat.
	Grams.	*Grams.*	*Grams.*
None	1.94	38.18	−40.99
76.12 grams cane sugar	1.45	43.19	− 8.41
104.97 grams cane sugar	1.07	47.78	+ .51
None	1.42	26.47	−28.10
42.96 grams starch	1.53	33.28	−10.54
None	2.00	31.53	−32.10
57.38 grams starch	1.52	39.67	−10.74

CARBOHYDRATES AND FEED FAT.

Rubner substituted dextrose for fat in the diet of a dog receiving also a fixed amount of lean meat. The results of this substitution are given in the following table, and show that with the larger amount of dextrose in place of the fat previously fed the loss of body fat was prevented:

Replacement of feed fat by carbohydrates—Rubner.

Ration.	Feed per day.			Gain or loss by animal.	
	Meat.	Fat.	Dextrose.	Nitrogen.	Carbon.
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Meat and fat	300	42		+1.81	+1.27
Do	300	50		+ .10	+9.31
Meat and dextrose	300		63.7	+1.78	−7.44
Do	300		79.7	+2.28	−8.15
Do	300		115.5	+1.98	+6.21

FEED PROTEIN AND BODY FAT.

It has already been shown that body protein may replace body fat in the katabolism of the fasting animal. A similar substitution of feed protein for body fat may take place. When protein is given to a previously fasting animal it is a well-known fact that the nitrogen of the protein is rapidly split off and excreted, while the nonnitrogenous portion of the molecule serves as a source of energy to the organism. (Compare pp. 78 to 82.) This nonnitrogenous residue can be substituted for body fat, as is illustrated in an experiment by Rubner in which extracted lean meat was given to a fasting animal, with the result tabulated below:

Replacement of body fat by protein—Rubner.

	Nitrogen of food.	Nitrogen katabolized.	Fat katabolized.
	Grams.	*Grams.*	*Grams.*
Fasting	0	5.25	84.39
Fed	35.22	26.37	28.37
Difference		+21.12	−56.02

FAT OR CARBOHYDRATES AND PROTEIN.

A certain minimum of protein is essential to the maintenance of the protein tissues of the body, but feed protein in excess of this amount undergoes rapid katabolism and serves substantially as a source of energy. Such an excess of protein in the feed can be replaced by nonnitrogenous nutrients, particularly the carbohydrates. This effect of fat or carbohydrates as a substitute for protein may be illustrated by the following tabulation of the average results of a number of Pettenkofer and Voit's experiments:

Replacement of feed protein by fat or carbohydrates—Pettenkofer and Voit.

Rations.	Feed per day.				Gain or loss by body.	
	Meat.	Fat.	Starch.	Grape sugar.	Nitrogen.	Carbon.
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Protein only:						
Series I	1,500				0	+ 3.3
Average of all (22 experiments)	1,500				+0.6	+ 8.7
Protein and fat:						
100 grams fat (1 experiment)	500	100			+ .3	+27.1
200 grams fat (5 experiments)	500	200			− .6	+67.3
Protein and carbohydrates:						
Starch (8 experiments)	500	5.3	200		−1.8	+ 9.0
Grape sugar (3 experiments)	500			200	−1.3	+ 7.2

It appears, then, that all the principal nutrients may serve to supply energy to the body, and the facts just considered show a remarkable degree of flexibility on the part of the animal organism as regards the nature of the material which can be utilized for its metabolism. Aside from the small minimum of protein required, the metabolic activities of the body may be supported now at the expense of the stored body fat, now by the body protein, and again by the protein, the fats, or the carbohydrates of the feed. Whatever may be true economically, physiologically the welfare of the mature animal is not conditioned upon any fixed relation between the classes of nutrients in its feed supply apart from the minimum requirement for protein.

AVAILABILITY OF ENERGY.

Since the chief function of the feed, aside from a minimum of protein, is to supply energy, it would be natural to suppose that the quantity of energy liberated in the body by the oxidation of any given substance (i. e., its metabolizable energy) would be the measure of its nutritive value. If one gram of starch, for example, can liberate 4.2 calories of energy in the body and a gram of fat 9.5 calories, apparently the relative values of the two should be in proportion to these figures. But while the metabolizable energy of the feed represents the maximum amount of energy which can be extracted from it by the organism, it does not follow that all of it can be utilized for maintenance. Energy is not something which can be fed into the organism regardless of its source, like fuel under a boiler. Whatever energy is in essence, so far as the animal is concerned it is carried as chemical energy by the compounds of the feed, and these must be such as can take part in the actual chemical changes occurring in the cells if their energy is to be utilized. The body can not, like a heat engine, avail itself of energy in the kinetic form. It is quite conceivable that a compound might be resorbed from the digestive tract and then simply oxidized to get rid of it without its entering into the cell metabolism. Its energy would be metabolized, that is, converted into the kinetic form, but it would be simply a source of heat and not of other forms of energy. Somewhat similar is the case of the chemical changes occurring in the digestive tract. Some of these, notably the fermentations of the feed, set free energy as heat, yet this energy plays no part in the actual metabolism of the tissues. It is clear, then, that we are not warranted in concluding that because, for example, a fasting animal breaks down body substance equivalent to 10 therms per day, therefore a ration containing 10 therms of metabolizable energy will suffice to maintain the animal. That will depend upon how completely the body is able to use the 10 therms of metabolizable energy supplied to it. In other words, the energy must not only be present, but it must be available energy.

If the metabolizable energy were all available to protect body tissue from oxidation, then giving feed to a fasting or partially fasting animal would be practically the substitution of one kind of fuel for another, and the total heat production would remain the same. It is, however, an observation as old as the time of Lavoisier that the consumption of feed tends to increase the heat production of an animal. That investigator observed the oxygen consumption of man to increase materially (about 37 per cent) after a meal, and subsequent experiments by a large number of investigators have fully confirmed these earlier results, so that the fact of an increased metabolism consequent upon the ingestion of feed is undisputed. It is especially to the investigations of Zuntz and his associates that we owe the unquestionable demonstration of this fact and of its significance in relation to the nutritive values of feeding stuffs.

These relations may perhaps be more clearly apprehended through an illustration taken from actual experimental work.

AVAILABILITY FOR CATTLE.

In an experiment by Armsby and Fries[1] a steer averaging 373.7 kilograms live weight was fed daily 3.2 kilograms of timothy hay, an amount known to be insufficient for maintenance. The potential energy contained in the feed, the losses in the various excreta, and the metabolizable energy of the ration were determined, with the following results:

Per day and head.

Feed:		Therms.
3.199 kilos timothy hay		12.618
Excreta:	Therms.	
4.786 kilos feces	5.247	
3.943 kilos urine	.627	
0.079 kilo methane	1.057	
Total		6.931
Metabolizable energy of ration		5.687

A balance experiment with the respiration calorimeter showed, as was expected, that the steer was living in part at the expense of his own tissues, the total loss of protein and fat being equivalent to 2.377 therms[2] per day.

In the period immediately following this one the same steer ate per day 5.194 kilograms of the same timothy hay, all the other conditions of the experiment being as nearly identical as possible. The metabolizable energy of this larger ration, determined in the manner just indicated, was 9.262 therms,[3] while a balance experiment showed that the loss of protein and fat had been reduced to the equivalent of 0.357 therm.[3]

The following comparison of the two periods can therefore be made:

Available energy of timothy hay.

	Ration.	Metabolizable energy of ration.	Energy of fat and protein lost by animal.
	Kilos.	*Therms.*	*Therms.*
Timothy hay	5.294	9.262	0.357
Do	3.199	5.687	2.377
Difference	2.095	3.575	2.020

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[1] Bureau of Animal Industry, Bulletin 128, pp. 177 and 184.

[2] Computed to 12 hours' standing.

[3] Corrected to the same live weight as in Period III.

On the lighter ration, the steer supplemented the energy derived from its feed by 2.377 therms derived from the katabolism of its own fat and protein, but when 2.1 kilograms of timothy hay was added to the ration, the amount of energy which had to be furnished by the body tissues was reduced to 0.357 therm. In other words, 2.1 kilograms of timothy hay supplied 2.020 therms of energy which was available to support the necessary bodily activities and which, therefore, could replace an equal amount which would otherwise have been derived from the katabolism of body substance. This was the contribution which this amount of hay made to the maintenance of the steer.

But the 2.1 kilograms of timothy hay added to the ration supplied, as the table shows, 3.575 therms of metabolizable energy. Clearly, then, a unit of metabolizable energy supplied by the digestible matter of the hay was less efficient than the same amount supplied by body substance. Only 56.5 per cent of it could be substituted for that previously supplied by the katabolism of the fat and protein of the body of the steer, while the remaining 1.555 therms, or 43.5 per cent, simply increased the heat production of the animal, the latter being as follows:

Daily heat production.[1]

	Therms.
On the heavier ration	9.619
On the lighter ration	8.064
	1.555

It is customary in such a case to speak of the 2.020 therms as the available energy of the hay added to the basal ration of Period III and to say that 56.5 per cent of the metabolizable energy of the hay was available. Such a method of statement does not necessarily imply that the remaining 43.5 per cent served no useful function in the body, but simply asserts that the net result to the organism was the same as if 56.5 per cent of the metabolizable energy were substituted unit for unit for energy derived from the katabolism of body substance and as if the remaining 43.5 per cent were useless. What the experiment really shows is that a unit of metabolizable energy in the hay had only 56.5 per cent of the value for maintenance of a unit of metabolizable energy in the body substance (chiefly fat) previously katabolized, but the first method of expression is both common and convenient and may be retained.

Experiments by the same authors on several other feeding stuffs have given results of the same general character as those just quoted. Of the metabolizable energy of these feeding stuffs, as directly determined in each ex-

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[1] Corrected to 12 hours standing.

periment, the following percentages were found to be available in the above sense, while the remainder simply served to increase the heat production:

Average availability of metabolizable energy.

	Per cent.
Timothy hay, 5 experiments	56.32
Clover hay, 2 experiments	58.47
Corn meal, 1 experiment	69.12
Wheat bran, 2 experiments	55.36
Mixed grain (1 part wheat bran, 3 parts corn meal, 3 parts linseed meal O. P.), 4 experiments	57.42

Kellner's[1] extensive investigations upon the metabolism of fattening cattle have likewise demonstrated that in the productive feeding of these animals only part of the metabolizable energy supplied in excess of the maintenance ration is recovered in the gain produced, the remainder being converted into heat, so that the heat production increases with the amount of feed consumed.

AVAILABILITY FOR THE HORSE—ZUNTZ AND HAGEMANN'S RESULTS.

The foregoing results upon cattle have been cited because they illustrate simply and clearly the basic conception of the availability of feed energy and also because they are, so far as the writer is aware, the first experiments upon farm animals on submaintenance rations in which the complete balance of matter and of energy for 24 hours has been determined. Zuntz and Hagemann[2], however, had shown several years before in an extensive investigation that the increased metabolism which Zuntz and his associates had observed in dogs and men as resulting from the ingestion of food was even more marked in the case of the horse.

In their investigations the respiratory exchange of the animal was determined by the Zuntz method in short periods at various intervals after the consumption of more or less diverse rations, a small correction being added for cutaneous and intestinal respiration. By combining these results with those of a number of separate digestion trials in which the nitrogen and carbon of the feed and of the visible excreta were determined, an approximate determination of the total energy metabolism of the animal was also possible.[3]

For example, on the average of a number of experiments in which the metabolism shortly before feeding in the morning, shortly after feeding, and some hours later was determined by the methods just outlined, the following results, computed per kilogram per minute were obtained.[4]

	Oxygen consumed.	Energy liberated.
	c. c.	*Gram-calories.*
Fasting	3.339	16.929
36 minutes after feeding	3.648	18.510
3½ hours after feeding	3.704	18.787

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[1] Die Landwirtschaftlichen Versuchs-Stationen, Band 53, and Ernährung der Landwirtshaftlichen Nutztiere.

[2] Landwirtschaftliche Jahrbücher, vol. 27, Ergänzungsband III.

[3] For a more complete account of the method, compare Armsby, Principles of Animal Nutrition, pp. 386–387.

[4] Loc. cit., p. 282.

It was also found that coarse fodder (hay) produced a much more marked effect than did grain. The following comparison of the average of the experiments of period *c* on an exclusive hay diet with that of the experiments of period *f* on a mixed ration illustrates this fact.[1]

	Period *c*.	Period *f*.
Time since last fed .... hours..	2.6	2.8
Ration:		
Hay .... kilos..	About 10.5	4.75
Oats .... do....	....	6.00
Straw .... do....	....	1.00
Total digested nutrients (fat × 2.4) .... grams..	4,125	5,697
Per kilogram and minute:		
Oxygen consumed .... cubic centimeters..	3.9837	3.6986
Carbon dioxid given off .... do....	3.6586	3.6695
Energy set free (computed) .... gram-calories..	19.552	18.339
Energy katabolism per day and head .... calories..	12,450	11,678

DIGESTIVE WORK FOR CRUDE FIBER.

Zuntz and Hagemann estimate the fuel value of the total digestible nutrients in the feed of the horse (including digestible crude fiber and digestible fat × 2.4) at 3.96 calories per gram, and on the basis of experiments on man made by Magnus-Levy in Zuntz's laboratory they assume that 9 per cent of the metabolizable energy of the digestible nutrients as thus computed is expended in their digestion. The hay ration of the foregoing table contained 1,572 grams less of (estimated) digestible nutrients than the mixed ration. The corresponding expenditure of energy in the digestion of these nutrients (9 per cent of their metabolizable energy) equals 580 calories. Accordingly the energy katabolism should have been 580 calories less in period *c* than in period *f*. It was actually 772 calories greater, a difference of 1,352 calories. This difference is ascribed to the presence in the hay ration of 648 grams more of total crude fiber and corresponds to 2.086 calories per gram of the latter.

WORK OF MASTICATION.

The foregoing computations relate to the expenditure of energy in the digestion of the food after it has entered the stomach. The same authors have also determined the increase in the gaseous exchange caused by mastication, deglutition, etc. For this purpose they compare[2] the excretion of carbon dioxid and the consumption of oxygen during the time actually occupied in eating with the corresponding amounts during rest, as shown by the average of a number of experiments made under identical conditions. On the assumption that the protein metabolism is unaltered, the amounts of carbohydrates and fat metabolized and the corresponding amounts of energy are calculated. The following is a summary of the results computed per kilogram of feed:

Energy expended in mastication of 1 kilogram—Zuntz and Hagemann.

Feed.	Number of experiments.	Oxygen consumed.	CO_2 excreted.	Equivalent energy.
		Liters.	*Liters.*	*Calories.*
Oats and cut straw (6:1)	8	12.964	10.679	64.17
Hay	8	33.840	27.813	167.44
Hay, oats, and cut straw	8	20.072	17.677	100.79
Maize and cut straw (6:1)	2	7.133	6.205	35.72
Green alfalfa	7	6.171	4.980	30.42
Computed for oats alone	....	....	....	47.00
Computed for maize alone	....	....	....	13.80

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[1] Loc. cit., pp. 276–279.

[2] Loc. cit., p. 271.

As was to have been expected, the work of mastication proves to be much greater in the case of hay than in that of grain. Maize gave a remarkably low result, while the lowest was obtained with green fodder. Even when the results on the latter are computed per kilogram of dry matter, they are still about 40 per cent lower than those on hay. A few experiments on old horses with defective teeth gave somewhat higher results for the mixture of oats and cut straw.

While pointing out that, as the above results show, other factors than the amount of crude fiber influence the work of mastication, they nevertheless believe that a sufficiently close approximation for practical purposes may be reached by computing the work of mastication upon the amount of crude fiber present, which gives an average of 0.565 calorie per gram, and using this factor to compute the work of mastication of the average ration. Adding this factor to the 2.086 calories computed for the work of digestion of one gram of fiber gives a total of 2.65 calories per gram of total crude fiber as representing the work of mastication together with the extra expenditure of energy in digestion.

COMPUTATION OF AVAILABLE ENERGY.

In brief, then, Zuntz and Hagemann compute the available energy, or maintenance value, of a feeding stuff for the horse as follows: First, the metabolizable energy is computed at the rate of 3.96 calories per gram of total digestible matter, including the digestible crude fiber and the digestible fat multiplied by 2.4. Second, from the metabolizable energy thus computed there is subtracted 9 per cent for the work of digestion and in addition 2.65 calories for each gram of total crude fiber present.

The method of computation may be conveniently illustrated from the data given by Langworthy[1] for timothy hay. Zuntz and Hagemann's factors, recalculated per pound for convenience, become, for metabolizable energy, 1.796 therms; for crude fiber, 1.202 therms. On this basis the calculation of the available energy of the hay would be as follows:

Available energy in 100 pounds of timothy hay.

Digestible nutrients:	Pounds.	
Protein	1.25	
Crude fiber	12.39	
Nitrogen-free extract	21.29	
Fat (1.18×2.4)	2.83	
	37.72	
Total crude fiber	29.00	
		Therms.
Metabolizable energy (1.796 therms×37.72)		67.75
Work of digestion:	Therms.	
9 per cent of metabolizable (67.75 therms×0.09)	6.10	
Additional for crude (1.202 therms×29)	34.86	
Total		40.96
Available energy (maintenance value)		26.79

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[1] U. S. Department of Agriculture, Office of Experiment Stations, Bulletin 125, p. 14.

As is evident from the brief description given of the methods by which the factors are reached, this method of computation is not claimed by its authors to be scientifically exact, but they believe it to be a sufficiently close approximation on which to base computations of rations in practice.

Zuntz and Hagemann's conclusions have been subjected to considerable criticism, the two principal points being, first, their estimate of 9 per cent for the work of digestion, based upon the results of experiments on man; and, second, and more especially, the assumption that the metabolism for 24 hours may be computed from the results of comparatively short respiration experiments. Qualitatively, Zuntz and Hagemann have clearly demonstrated the very considerable expenditure of energy by the horse in the digestion of his feed, as well as the fact that this expenditure is much greater with coarse fodders than with grain, and they were the first to point out that this expenditure of energy must be taken account of in estimating the values of feeding stuffs. There may be a difference of opinion as to the quantitative worth of their figures, and certainly investigations by more direct methods, involving fewer assumptions and complex calculations, are greatly to be desired, but until such results are obtained we may continue to use provisionally those reached in the manner just described.

AVAILABILITY FOR THE HORSE—WOLFF'S RESULTS.

His extensive investigations upon the working horse, made at Hohenheim in 1877 to 1894[1] and antedating the investigations thus far mentioned, led Wolff to a still simpler approximate method of estimating what in a sense corresponds to the available energy ot the feed of the horse.

In Wolff's experiments, the horse performed a measured amount of work which was so adjusted in different periods as to be as nearly as possible in equilibrium with the feed consumed. This was considered to be the case when the live weight of the animal remained substantially unchanged for a considerable period and when the urinary nitrogen did not show an increase as a consequence of the additional work done. By comparing the work performed on a basal ration with that which could be done with a heavier one, the ratio of the work done to the additional feed consumed was established within the limits of error of the method, this being the prime object of the experiments. This being determined, however, it was a simple matter to compute the amount of feed corresponding to the total work done, while subtracting this from the total ration would give the maintenance ration. The results of these comparisons, made on the basis of the so-called "digestible nutrients" of the rations (the digestible fat being multiplied by 2.4) are considered on subsequent pages.

On the average of a considerable number of comparisons, it was found that the digestible nutrients from coarse fodders were less

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[1] Compare pp. 57 to 62.

efficient both for work production and for maintenance than were those derived from grain, and Wolff also cites the results of Grandeau and Le Clerc's experiments in Paris which show the same general result. Wolff shows, however, that if the digestible crude fiber be omitted from the comparisons, the ratio between fiber-free nutrients and the work performed is comparatively uniform and also that this assumption yields uniform results for the fiber-free nutrients required for maintenance. He therefore concludes that the crude fiber in the rations of the horse is apparently valueless and that the remaining digestible nutrients may be regarded as of equal value whether derived from grain or from coarse fodders. Expressed in the light of our present conceptions, this is practically equivalent to saying that the expenditure of energy in digestion is proportional to the metabolizable energy of the crude fiber, or that the available energy is proportional to the amount of fiber-free nutrients.

Wolff is careful to say that the digestible crude fiber is *apparently* valueless, and virtually regards the amount of crude fiber as furnishing a convenient empirical measure of the difference in the nutritive value of the digestible nutrients of coarse fodder as compared with those of grain. That such is the case is doubtless explained in part by the rather limited variety of feeding stuffs employed in the experiments. The coarse fodder was meadow hay, with, in some cases, a small addition of straw, while the grain was usually oats, partially replaced in some cases by other feeds. Whether the same relation between fiber-free nutrients and work done would hold in widely different rations is not apparent.

It should be borne in mind that in reality Wolff's results are relative only. They do not show the actual amount of available energy in the feed or ration, but only that it is proportional to the fiber-free nutrients. The energy of the latter would differ considerably from the available energy as computed by Zuntz and Hagemann's method, first, because it does not include the deduction of 9 per cent for digestive work; and, second, because it assumes a uniform value of zero for crude fiber, while Zuntz and Hagemann's method gives the crude fiber a negative value if it has a digestibility of less than 55 per cent. The values computed according to Wolff's method from the fiber-free nutrients are therefore considerably higher than Zuntz and Hagemann's figures.

AVAILABILITY FOR CARNIVORA.

For many years it was taught, in accordance with Rubner's theory of "isodynamic replacement" (compare p. 72), that with carnivora the nutrients were of value in proportion to their content of metabolizable energy. Rubner's own later investigations,[1] however, have

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[1] Die Gesetze des Energieverbrauchs bei der Ernährung.

shown that what is true of the feeding stuffs consumed by horses and cattle is also true of nearly pure nutrients fed to dogs. With these subjects it is possible to use the fasting state as the basis of comparison, which considerably simplifies the investigations. The experiments were made at a comparatively high temperature, namely, about 33° C., a fact which is of importance, as will appear later, in the interpretation of the results.

An experiment in which nearly enough fat was fed to supply the requirements of the organism for energy gave the following results per kilogram live weight, stated in a form which is somewhat different from that used by Rubner but which in substance is identical with it:

Availability of energy of fat—Rubner.

	Metabolizable energy of feed per kilogram live weight.	Loss by body per kilogram live weight.
	Calories.	*Calories.*
Fat fed	53.4	7.5
Fasting	0	54.0
Difference	53.4	46.5
Percentage available	87.08	

This result appears somewhat remarkable in view of the fact that the comparison is virtually with body fat. Literally interpreted, it means that the energy of feed fat is only 87 per cent as valuable as the energy of body fat plus a little protein. If this be true, it implies a larger expenditure of energy in the digestion of fat than now seems probable, since the katabolism of resorbed feed fat can hardly differ greatly from that of body fat. Rubner's figure is the result of a single experiment and unfortunately it enters into the computation of all the other results. A redetermination of this factor is much to be desired.

In two other experiments, lean meat nearly equivalent to the maintenance requirement was fed. The meat contained a small amount of fat, the average metabolizable energy of the feed per kilogram live weight being distributed as follows:

	Calories.
In protein	56.70
In fat	4.95
	61.65

Using the data afforded by the experiment on fat, the availability of the energy of the protein may be computed as follows:

Availability of energy of protein—Rubner.

	Metabolizable energy of feed per kilogram live weight.	Loss by body per kilogram live weight.
	Calories.	*Calories.*
Meat fed	61.65	8.90
Fasting	0	51.50
Difference	61.65	42.60
Difference due to fat	4.95	4.31
Difference due to protein	56.70	38.29
	Per cent.	
Percentage available	67.53	....

The difference between the percentage available and 100 shows, of course, the proportion of the metabolizable energy of the feed which was expended in increasing the total metabolism as measured by the heat production. This increase of the metabolism of the body is called by Rubner the "specific dynamic effect" of the several nutrients. Rubner's final average results are contained in the following table. It should be clearly understood that they are not applicable to the "digestible nutrients" of the feed of herbivora.

Average availability—Rubner.

	Availability.	Specific dynamic effect.
	Per cent.	*Per cent.*
Body protein	68.1	31.9
Meat protein	69.1	30.9
Gelatin	72.0	28.0
Fat	87.3	12.7
Cane sugar	94.2	5.8

CAUSES OF INCREASED METABOLISM.

The foregoing paragraphs have dealt with the fact of the increased metabolism and consequent heat production resulting from the ingestion of feed without considering the cause of the increase. Two explanations of it naturally suggest themselves. The first is that the greater supply of the various nutrients directly stimulates the metabolism of the body cells, while the second ascribes the increased metabolism to the additional expenditure of energy required for the digestion of the feed and its preparation for metabolism in the actual vital processes. The latter explanation is the one which has been generally accepted, although by no means without dissent,[1]

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[1] Compare Heilner, Zeitschrift für Biologie, vol. 48, p. 144; vol. 50, p. 488.

and the expenditure of energy for these purposes has been somewhat loosely and perhaps not altogether fortunately designated as the "work of digestion." A consideration of some of the processes connected with the consumption of feed which lead to the liberation of energy may serve to clarify the conception.

MECHANICAL WORK.

Digestion requires more or less mechanical work in the prehension and mastication of the feed and in moving it through the digestive organs. In this connection, too, it should be remembered that the feed in this sense includes the water as well, three or four parts of water being usually consumed by herbivora for each part of dry matter in the feed. As noted on p. —, Zuntz and Hagemann have compared the metabolism of the horse while eating with that of the same animal while at rest and computed from the difference the amount of energy expended in mastication. The following recapitulation of some of their results shows the number of calories of energy expended in the mastication of 1 kilogram of the material named:

	Calories.
Hay	167. 5
Green alfalfa	30. 4
Oats	47. 0
Maize	13. 8

Kellner[1] has investigated the effect of the grinding of straw upon its value in a productive ration. He finds that the practical elimination in this way of the work of mastication reduces the expenditure of energy by approximately 0.66 calorie for each gram of crude fiber present in the straw.

That the movement of the masticated feed through the digestive tract must also require an expenditure of energy is obvious, but no data are available as to its amount.

SECRETION.

The secretion of the digestive fluids likewise requires some expenditure of energy. This has been shown by direct experiment to be true of the salivary glands and the pancreas and is also true, doubtless, of the other digestive glands. Apparently, however, the amounts of energy thus expended are comparatively small.

FERMENTATION.

The extensive fermentations occurring in the digestive tract of herbivora result in a considerable evolution of heat. The most important of these is the methane fermentation. Assuming on the basis of Tappeiner's results[2] that 100 grams of carbohydrates yield 4.7 grams of methane and 33.5 grams of carbon dioxid, and assuming further that two-thirds of the carbon of the organic acids produced is contained in acetic acid and the remainder in butyric, it may be computed that the heat evolved amounts to 12.5 per cent of the total energy of the digested carbohydrates or 0.523 calorie per gram. It should be noted that this estimate does not refer to the potential energy carried off in the methane, but to the heat evolved in the fermentation. The latter is part of the metabolizable energy of the carbohydrates, since it is liberated in the

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[1] Die Ernährung der Landwirtschaftliche Nutztiere, 5th ed., p. 163.

[2] Zeitschrift für Biologie, vol. 20, p. 52.

kinetic form in the body, but since it takes at once the form of heat, it is not available energy in the sense in which the term is here used.

The same general considerations, of course, apply to the other fermentations and putrefactions which occur in the digestive tract, but their amount in herbivora is probably small compared with that of the methane fermentation, and we have relatively little knowledge regarding them.

DIGESTIVE CLEAVAGES.

It is well known that extensive cleavages of the feed ingredients occur in the digestive tract. The nutrients, by the action of the digestive ferments, are split up into simpler atomic groupings—the so-called building stones of the molecule—out of which the proteins, carbohydrates, and fats peculiar to the animal body are built up. One argument which has been brought forward in the past against the extensive occurrence of such cleavages in natural digestion, especially of the proteins, has been the teleological one that the splitting up into these comparatively simple compounds was a waste of valuable nutritive material. On the other hand these processes have been invoked to explain the striking effect of the proteins in stimulating the metabolism—their large specific dynamic effect, to use Rubner's terminology. So far as the peculiar use of protein in the body is concerned, it is well established that its crystalline cleavage products can be resynthesized to form protein. It is of special interest, therefore, to learn that these cleavages and resyntheses are apparently nearly isothermic processes. Some of the cleavage products of protein contain more potential energy per gram than protein itself, as, for example, leucin, with 6.525 calories per gram, and tyrosin, with 5.916 calories per gram. Others, like alanin, with a heat of combustion of 4.356 calories, contain but little less energy than the protein from which they are derived. Even the simplest amino-acid, glycocol, resulting from this cleavage has a heat of combustion of 3.129 calories per gram. The impression which these figures give—that but little energy is lost in the cleavage of the proteins—is confirmed by direct experiments. Loewi[1] found the dry residue of the tryptic digestion of meat to have an energy value of 4.6 calories per gram. Tangl, Lengyel, and Hari[2] found the products of the peptic or tryptic digestion of egg albumin and serum albumin to contain nearly or quite as much potential energy as the original protein. Grafe[3] has made artificial digestions of protein in a calorimeter, and found no noticeable evolution or absorption of heat. It seems safe, therefore, to regard the digestive cleavage of protein as at least a nearly isothermic process, causing little loss of energy in digestion.

Substantially the same thing is true of the digestive cleavage of carbohydrates and fats. Thus 1 gram of starch yields 1.111 grams of dextrose, and the heats of combustion of these quantities are, respectively, 4.183 calories and 4.159 calories, showing a loss of less than 0.6 per cent. One gram of sucrose yields 0.5264 gram each of dextrose and levulose, and the energy values are, respectively, 3.955 calories and 3.947 calories, or a loss of less than 0.2 per cent So, too, 1 gram of tristearin with a heat of combustion of 9.43 calories yields by hydrolysis 0.9573 gram of stearic acid, equivalent to 9.026 calories, and 0.1033 gram of glycerin, equivalent to 0.424 calorie, or a total of 9.45 calories.

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[1] Leathes. Problems in Animal Metabolism, p. 129.

[2] Archiv für die gesammte Physiologie des Menschen und der Thiere (Pflüger), vol. 115, p. 1.

[3] Jahresbericht über die Fortschritte der Tier Chemie, vol. 37, p. 917.

INTERMEDIARY METABOLISM.

The chemical reactions taking place during the so-called intermediary metabolism of the resorbed material before it is finally utilized for the vital processes have also to be considered as possible sources of heat production, although our present knowledge of them is meager.

This possibility is of special interest in connection with the marked effect of protein on the energy metabolism, since this can hardly be ascribed to digestive work in the strict sense. In the normal digestion of protein fermentations play a very small part, while, as just shown, the digestive cleavage of protein is substantially isothermic. Neither can we imagine that the mechanical work of digestion or the secretion of digestive juices can account for the large expenditure of energy. Rubner[1] has reported experiments in which the protein katabolism of the fasting animal was artificially increased by the administration of phlorhizin, and in which a similar increase in the heat production is computed, although there could have been no digestive work in the strict sense. Falta, Grote, and Stählein[2] have found that the products of the tryptic digestion of casein when fed to a dog produce nearly as great an increase in the metabolism as does a corresponding amount of casein, while in the familiar experiments of Zuntz and Mering[3] the intravenous injection of the crude products of the peptic digestion of blood fibrin had a like effect.

The katabolism of protein seems to consist in outline, first, of a hydrolytic cleavage into peptids and amino-acids and, second, in a deamidization of these latter compounds, and it is the nonnitrogenous products resulting from this deamidization which serve as a source of energy for the body, the nitrogen being split off as ammonia and excreted as urea. It is to a liberation of energy in the form of heat in these preliminary processes of preparing protein to serve as fuel that Rubner and other authors ascribe its specific dynamic effect.

Our knowledge of the intermediary metabolism of protein is too meager to render any quantitative estimate of the amount of energy lost in this way of much value. The cleavage of protein, as noted, seems to be substantially isothermic. The deamidization of the simpler amino-acids with a small number of carbon atoms seems at first thought to involve considerable loss of energy. For example, the potential energy of 1 gram of glycocol and of alanin and of equivalent amounts of acetic and propionic acids are:

	Glycocol.	Alanin.
	Calories.	*Calories.*
Energy of amino acid	3.129	4.356
Energy of equivalent fatty acid	2.791	4.129
Difference	.338	.227
Percentage loss	10.8	5.2

A similar comparison of alanin with the equivalent amount of lactic acid shows an apparent loss of about 14 per cent. With the higher members of the series, the loss computed in this way is relatively small. It must be remembered, however, that the amino group is split off as ammonia, which also con-

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[1] Gesetze des Energieverbrauchs bei der Ernährung.

[2] Beiträge zur Chemischen Physiologie und Pathologie, vol. 9, p. 372.

[3] Archiv für die gesammte Physiologie des Menschen und der Thiere (Pflüger), vol. 32, p. 199.

tains potential energy equal, according to Ostwald, to 3.319 calories per gram in the gaseous state. If we assume that the alanin yields lactic acid with a heat of combustion of 3.7 calories per gram we may make the following comparison:

	Calories.	Calories.
Energy of 1 gram alanin		4.356
Energy of 1.011 grams lactic acid	3.742	
Energy of 0.191 gram ammonia	0.634	
		4.376
Difference		.020

In other words, it would appear that the deamidization of the amino acids, like the antecedent cleavage of the proteins, is a nearly isothermic reaction and that we must seek elsewhere for the explanation of the specific dynamic effect of protein. We can by no means assert, however, that the protein katabolism actually takes place according to this simple scheme, nor that the nonnitrogenous substances resulting from deamidization of the amino acids yield their energy without loss. It seems not unlikely that the higher fatty acids and other nonnitrogenous derivatives of protein are broken down by cleavage and otherwise to comparatively simple molecules before they are finally oxidized, and there is the possibility of more or less loss of energy in such processes.

As already indicated, Rubner explains the specific dynamic effect of protein from the foregoing point of view, but in a different manner. It has been shown beyond reasonable doubt that sugar is produced, or may be produced, in the katabolism of protein. According to Rubner, it is only the energy of this sugar that is capable of being used for the physiological functions of the body cells, while the energy set free in the conversion of protein into sugar is liberated as heat and constitutes the specific dynamic effect. This explanation of Rubner's, however, seems to be disproved by recent results reported by Lusk and Ringer.[1] They have shown that alanin is completely convertible to dextrose in a diabetic animal, while in the case of glutamic acid but three out of the five carbon atoms of the molecule are utilized for the production of dextrose. According to Rubner's hypothesis, therefore, alanin should show no specific dynamic effect, while glutamic acid should show a considerable one. In a preliminary communication Lusk[2] reports that neither one of these amino acids when added to a standard diet increased the excretion of carbon dioxid in the respiration. This result is in striking contrast with those of Falta, Grote, and Stählein and of Zuntz and Mering just referred to, in which the crude products of tryptic or peptic digestion were fed. They suggest that some substance other than the recognized amino-acids may be responsible for the stimulating effect of protein upon metabolism, while they likewise recall the fact that crude peptones have been found to have a poisonous effect when injected intravenously while purified peptones do not, and likewise the fact that in Zuntz and Mering's experiments purified peptones caused no increase in the metabolism.

EXCRETION.

Zuntz[3] calls attention to Barcroft's[4] experiments, which show that the excretory activity of the kidneys is accompanied by a notable increase in the amount of oxygen consumed, and sees in the work thrown on these organs by the elimination of the nitrogen of protein one of the causes of its specific

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[1] Journal of the American Chemical Society, vol. 32, p. 671.

[2] Proceedings of Society for Experimental Biology and Medicine, 1910, vol. 7, p. 136.

[3] Medizinsche Klinik, 1910.

[4] Ergebnisse der Physiologie, vol. 7, p. 744.

dynamic effect. In experiments in collaboration with Steck he found that a marked increase of the metabolism, as computed from the oxygen consumed, followed the administration of urea, and likewise of sodium chlorid, to men and dogs. In the case of urea he computes that the effect was equal to 20 to 25 per cent of that of an equivalent amount of protein. Zuntz also calls attention to earlier experiments by Nering and Schmoll in which carbohydrates added to the diet of a diabetic produced a similar increase of metabolism, although the sugar was not assimilated but excreted unchanged. Zuntz ascribes the results obtained by Rubner to the fact that phlorhizin added largely to the increased excretory work required by the elimination of the nitrogen and of the sugar formed, pointing out also that Rubner has overestimated the amount of heat produced through failure to deduct the energy of the sugar excreted in the urine. On the other hand, in Lusk's experiments, just quoted, there was an increased excretion of urea subsequent to the administration of amino acids, but no increase in the carbon dioxide excreted, while Tangl[1] finds that the intravenous injection of urea or sodium chlorid causes an increase in the metabolism even when the kidneys have been extirpated or clamped off.

On the whole, it can not be said that any fully satisfactory explanation has yet been offered of the effects of feed, and in particular of protein, upon the metabolism, although certain factors, especially in domestic animals, are clearly evident.

But whatever explanation we may accept—whether, following Zuntz, we speak of work of digestion, or, with Rubner, avoid any implication as to the cause by the use of the term specific dynamic effect—the fact that the metabolizable energy of different feeding substances is not equally available for maintenance is established beyond question, and it is this fact which is of immediate importance in considering the energy requirement for maintenance and the maintenance values of feeding stuffs.

THE MAINTENANCE RATION.

In accordance with the principles laid down in the foregoing paragraphs, a maintenance ration as regards energy may be defined as one which supplies available energy equal to the fasting katabolism.

For example, in Rubner's experiment cited on page 27, in which fat was fed, the fasting katabolism of the dog was 54 calories per kilogram. Fat containing 53.4 calories of metabolizable energy diminished the loss of body tissue by 46.5 calories. Evidently, then, to reduce the loss by 54 calories, that is, to reduce it to zero, would have required $53.4\times\frac{54}{46.6}=62$ calories of metabolizable energy to be supplied in fat. The same thing may also be expressed in a slightly different way: If, as there computed, only 87.08 per cent of the metabolizable energy of fat is available, then to make good a total loss of 54 calories will require $54\div0.8708=62$ calories of metaboliza-

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[1] Biochemische Zeitschrift, vol. 34, p. 1.

ble energy in fat.[1] On this basis we may compute from Rubner's final averages (p. 28) that to maintain the dog experimented on, that is, to make good the loss of 54 calories of energy per kilogram, it would have been necessary to supply per kilogram the following amounts of metabolizable energy in the materials named:

	Calories.
In meat protein	79.3
In gelatin	78.1
In fat	61.9
In cane sugar	57.3

These figures afford a simple illustration of the fact that the amount of metabolizable energy required for maintenance is variable, being greater as its availability is less. The maintenance requirement of the dog was 54 calories of available energy. The maintenance ration needed to supply this varied according to the material which served as the carrier of the energy.

The same relations hold good for farm animals, although the fact that we can not well observe their fasting katabolism directly makes the computation a trifle more complicated. As an example, we may take the experiment on timothy hay already cited on page 20. The addition of 2.1 kilograms of timothy hay, equivalent to 3.575 therms of metabolizable energy, to the basal ration reduced the loss of energy from the body of the animal by 2.020 therms. Evidently, then, to have reduced it by 2.377 therms, that is, to zero, would have required the addition of $2.1 \times \frac{2.377}{2.020} = 2.471$ kilograms of the hay, equivalent to 4.207 therms of metabolizable energy. The total maintenance ration of this particular feeding stuff, then, would have been the basal ration plus this amount, or 5,670 kilograms of the hay, equivalent to 9.894 therms of metabolizable energy.

The same result may also be obtained by the use of the percentage availability as computed, viz, 56.5 per cent. The heavier ration failed to maintain the animal by 0.357 therms, that is, it lacked this amount of available energy. To supply this requirement would evidently demand $0.357 \div 0.565 = 0.632$ therms of metabolizable energy, which added to the 9.262 therms already contained in the ration gives a total as above of 9.894 therms. The same computation can, of course, be made from the lighter ration with the same result.

From the data given it is likewise possible to compute what the loss by the body would have been had it been practicable to withdraw all feed. The basal ration contained 5.687 therms of metabolizable energy, of which 56.5 per cent was available; that is, the basal ration was capable of preventing the loss of $5.687 \times 0.565 = 3.213$ therms from

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[1] On the assumption, of course, that the effect is a linear function of the amount of food.

the body. Had the basal ration been entirely withdrawn, then the loss would have been increased by this amount; that is, the total loss would have been 3.213+2.377=5.590 therms. The same quantity would, of course, be obtained by starting from the heavier ration or from the maintenance ration as computed above. The fasting katabolism, which can not well be determined directly, is thus obtained by computation. In other words, this steer expended daily 5.590 therms of energy in the maintenance of his necessary vital processes aside from those connected with the digestion and assimilation of his feed. This was his maintenance requirement as defined in the foregoing paragraphs, and an amount of the clover hay which was capable of supplying this quantity of available energy, viz, 5.670 kilograms, was a maintenance ration, while on smaller amounts he drew upon his body tissues to cover the deficiency.

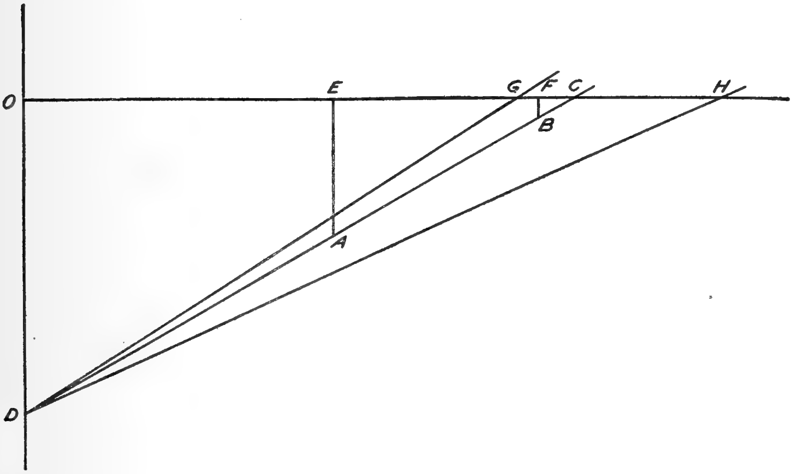

FIG. 1.—Availability of metabolizable energy of hay.

All these facts may also be conveniently represented graphically as follows:

If on the two coordinate axes of figure 1, we let the horizontal distances represent the metabolizable energy of the feed and the vertical distances the gain of energy by the body of the animal, the results of the two experiments just referred to may be represented by the points A and B, the distances OE (equal to 5.687 therms) and OF (equal to 9.262 therms) representing the amounts of metabolizable energy in the two rations and the distances EA (equal to —2.377 therms) and FB (equal to —0.357 therm) the corresponding (negative) gains of energy by the animal. A straight line drawn through A and B and intersecting the two axes at D and C will then represent the relation between the supply of metabolizable energy in the feed and the grain by the body of the animal.[1] This relation may also be expressed analytically by the equation $y=ax-m$, in which m=OD (equal to 5.590 therms) will represent the com-

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[1] Assuming that this is a linear function.

puted fasting katabolism and *a* the tangent of the angle between AB and the horizontal axis (equaling in this case 0.565), or the percentage availability, while OC (equal to 9.894 therms) is the maintenance ration in terms of the metabolizable energy of this particular hay.

The fasting katabolism being a constant quantity under like conditions, it follows that an amount of any feed capable of supplying 5.590 therms of available energy would have been a maintenance ration for this animal. It is clear then that the actual weight of feed required for maintenance will vary inversely as the availability of its energy. With this particular hay, it would have been necessary to use an amount containing 9.894 therms of metabolizable energy. With the timothy hay used in an earlier experiment, however, 62.9 per cent of whose metabolizable energy was found to be available, corresponding to the line DG in figure 1, it would have been necessary to use a quantity containing only 5.590÷0.629=8.888 therms, represented in the figure by OG, in order to supply the requisite available energy and secure maintenance. On the other hand, with a coarser forage having, e. g., an availability of only 45 per cent, represented by DH, it would have been necessary to supply 5.590÷0.45=12.420 therms of metabolizable energy, represented in the figure by the line OH. Just as was illustrated previously in the case of the dog, while the real requirement of energy for the vital processes remains unchanged the amount of feed necessary for maintenance is variable, depending upon the availability of its energy.

If with Zuntz we regard the increased katabolism consequent upon taking feed as representing energy expended in its digestion and assimilation, we may state the case in a slightly different way. We may compare the work thus done to the work of placing the fuel under a factory boiler. If this is done by means of power derived from the same boiler, it is evident that the farther the fuel has to be moved and the greater the amount of incombustible waste which it contains, the larger will be the fraction of the total boiler power required simply to keep the fire going and the less the proportion available for running the factory. So in the body, the greater the amount of energy which must be expended on the food in order to prepare it for its functions in the body the less is the proportion of its energy which is available for carrying on the physiological processes.

RELATION OF MAINTENANCE REQUIREMENT TO LIVE WEIGHT.

Before taking up the specific maintenance requirements of farm animals, it is necessary to consider the influence of size and weight upon the maintenance requirement.

That large animals katabolize more matter and produce more heat than smaller ones requires no special proof. Experiment shows, however, that the difference is not proportional to size or weight, but that small animals have a relatively more intense metabolism than large ones, the amount being approximately proportional to the body surface, which, of course, is relatively greater in the smaller animal. The existence of such a relation was surmised by various writers, but we are indebted to Rubner[1] for the first quantitative investigation of this question. He determined the fasting katabolism of six dogs whose weights ranged from 3 to 24 kilograms. With the addition of earlier experiments by Voit on a still larger dog, the average results were as follows, the total katabolism being expressed in terms of computed energy.

Relation of fasting katabolism to weight and to surface—Rubner and Voit.

No. of animal.	Live weight.	Katabolism per kilogram, live weight.	Katabolism per square meter of body surface.
	Kilos.	*Calories.*	*Calories.*
I	30.66	36.66	1,046
II	23.71	40.91	1,112
III	19.20	45.87	1,207
IV	17.70	46.20	1,097
V	9.51	65.16	1,183
VI	6.44	64.79	1,120
VII	3.10	88.25	1,214

While not mathematically constant, the ratio between the fasting katabolism and the surface shows a close approximation to uniformity, and the same fact has been verified by a considerable number of subsequent experiments. Moreover, it has been shown[2] to be approximately true not only of animals of the same species, but of animals ranging in size from man to domestic fowls, and including also cold-blooded animals. A recent investigation by Kettner[3] upon 13 guinea pigs furnishes a striking illustration of this general uniformity.

Rubner explains the apparent dependence of the fasting katabolism on body surface as the consequence of the loss of heat from the body due to the cooling action of the environment, which would naturally be proportional to the surface. The fact, however, that not inconsiderable variations have sometimes been observed indicates that other factors than the elimination of heat are concerned, and apparently the true cause lies deeper. Not merely the heat production but all the important physiological activities of the body, including the expenditure of energy in locomotion, seem to be proportional to the

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[1] Zeitschrift für Biologie, vol. 19, p. 535.

[2] E. Voit. Zeitschrift für Biologie, vol. 41, p. 113.

[3] Archiv für (Anatomie und) Physiologie, 1909, p. 447.

body surface rather than to the weight, while the fact that the same law holds true for cold-blooded animals, which assume the temperature of their surroundings and which, therefore, are subjected to no demand for heat, points in the same direction. Apparently we have here a general biological law of which the proportionality between heat production and body surface is one expression.

The internal work of the animal, however, as measured by the fasting katabolism or the fasting heat production, constitutes, as we have seen, its maintenance requirement. The maintenance requirements of animals of different sizes, therefore, especially of those of the same species, are proportional to their surfaces.

COMPUTATION OF RELATIVE BODY SURFACE.

Few actual determinations of the body surface of animals have been made and almost none for farm animals, so that it is at present impossible to express with accuracy the metabolism of the latter animals per unit of surface. For purposes of comparison between individuals of the same species, however, another method serves to give at least approximate results. It is a familiar geometrical fact that the surfaces of two solids of the same shape (i. e., similar figures in the geometrical sense) are proportional to the two-thirds powers of their volumes. By regarding all animals of the same species as of the same shape and also as having the same specific gravity, so that their weights are proportional to their volumes, it is a very simple matter to compute their relative surfaces and the corresponding maintenance requirements. For example, a steer weighing 583 kilograms was found to have a computed fasting katabolism (i. e., maintenance requirement) of 8.671 therms. A steer weighing 500 kilograms, other things being equal, would have a maintenance requirement in proportion to its smaller surface. The latter would be to the surface of the larger animal, approximately, as $(500)^{\frac{2}{3}}$ is to $(583)^{\frac{2}{3}}$ and the maintenance requirement would therefore be $8.671 \times \left(\frac{500}{583}\right)^{\frac{2}{3}} = 7.878$ therms. In this way it is a simple matter to compute the relative maintenance requirements of different individuals without the necessity of expressing them per unit of surface.

Of course, such a comparison is only approximately correct. In the first place, it may be presumed that there are differences in the specific gravity of different individuals, although it may be doubted whether these differences are sufficiently great to be of much significance in this connection. Moreover, different animals are not of the same shape. The young animal differs in conformation from the older one, and the beef steer and the dairy cow, for example, are far from being geometrically similar. It would be of much interest to determine the relation of surface to weight in different species, types, and ages of domestic animals, but lacking such determinations the method of computation above outlined may probably be assumed to give a fair approach to the truth and is at any rate the only one available.

THE MAINTENANCE RATIONS OF FARM ANIMALS.

In endeavoring to formulate the maintenance rations of farm animals it is important to have a clear conception of the nature of the problem and to distinguish between its physiological and its economic aspects. The physiological conception of the maintenance requirement is the amount of energy required to carry on the absolutely necessary vital processes in a state of the most complete rest possible. It is the least amount on which life can be sustained; the physiological minimum; the base line for comparison. In actual practice, no such state of complete rest can be maintained for any length of time. There is necessarily superadded to the minimum physiological requirement the energy expended in a variety of ways, but especially in the numerous minor muscular movements which are unavoidable in the waking state, which may be summarized under the term incidental work. Some of the factors of this incidental work are discussed on subsequent pages. Physiologically, this additional energy is expended for production; the animal is doing work on its surroundings. Economically, however, the work done is of no value and the energy required to do it is, therefore, from that point of view, a part of the cost of maintenance. In practice, of course, it is not the physiological but the economic requirement which is of importance. The latter will necessarily be more or less variable according to the individuality of the animal and the conditions under which it is maintained, as will appear in the following discussion, and statements of maintenance requirements and rations should therefore indicate to such a degree as is possible the conditions to which they are intended to apply.

CATTLE.

The maintenance requirements of cattle have been more extensively studied than those of other species and it will be convenient to take them up first, using the data also as a means of illustrating the principles involved and the methods of investigation employed.

The estimate of the maintenance ration of cattle long current and still occasionally cited was based upon the investigations of Henneberg and Stohmann[1] in 1858. According to their results, a 1,000-pound steer required for maintenance about 8.16 pounds of digestible organic matter per day, equivalent to about 14.3 therms of metabolizable energy. In view of the rather high stable tem-

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[1] Beiträge zur Begründung einer rationellen Fütterung der Wiederkäuer, Heft I, pp. 17–188.

perature in these experiments, however, Wolff[1] when formulating his well-known feeding standards increased this amount to 9.1 pounds digestible organic matter, equivalent to about 15.9 therms of metabolizable energy. Numerous subsequent experiments,[2] however, showed quite clearly that this estimate was considerably too high but without affording a sufficient basis for its correction, and it is only since 1898 that really satisfactory data have been secured.

One general method of experimentation has already been illustrated in the computation on pages 34–35 of the maintenance requirement of a steer. In brief, it consists of comparing the losses of body energy by the animal when fed two different amounts of the same feed or combination of feeds, each being less than the maintenance ration, and computing from the difference the amount of energy required for simple maintenance.

Investigations by Armsby and Fries[3] include eight trials with three different animals substantially upon this plan. In the later experiments of the series a correction was made for differences in live weight in the different periods of each experiment and for differences in the amount of time spent standing and lying, the results being computed to 12 hours standing. The results here given for the earlier experiments have been corrected in the same manner and therefore differ somewhat from those originally reported. The following tabulation of the results shows also, for comparison, the percentage availability of the metabolizable energy of the feed and likewise the maintenance ration expressed in terms of metabolizable energy. The results in every case have been computed to a uniform live weight in proportion to the two-thirds power of the weight. It is to be noted that the experiments are upon coarse fodder (clover and timothy hay) exclusively, and that the animals were not fat.

Maintenance requirements and rations of steers—Armsby and Fries.

Years.	Animal.	Available energy for maintenance.		Percentage availability of metabolizable energy.	Metabolizable energy for maintenance.		Feed.
		Per 500 kilograms live weight.	Per 1,000 pounds live weight.		Per 500 kilograms live weight.	Per 1,000 pounds live weight.	
		Therms.	*Therms.*	*Per cent.*	*Therms.*	*Therms.*	
1903	I	6.483	6.076	50.88	12.742	11.942	Clover hay.
1904	I	7.812	7.321	80.24	9.736	9.124	Do.
1905	A	6.649	6.231	60.51	10.988	10.297	Timothy hay.
1905	B	7.532	7.058	55.21	13.642	12.784	Do.
1906	A	6.077	5.695	[57.05]	10.652	9.982	Do.
1906	B	6.806	6.378	[56.50]	12.046	11.288	Do.
1907	A	5.186	4.860	57.05	9.090	8.519	Do.
1907	B	6.931	6.496	56.50	12.267	11.497	Do.
Average of all		6.685	6.264	59.24	11.395	10.679	
Average, omitting 1904.		6.523	6.113	56.24	11.632	10.901	
Average, 1905–1907		6.531	6.121	57.14	11.447	10.728	

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[1] Landwirtschaftliche Fütterungslehre, 2d ed., 1877, pp. 132 and 196.

[2] The Maintenance Ration of Cattle, Pennsylvania Experiment Station Bulletin 42, pp. 12–21.

[3] Bureau of Animal Industry, Bulletins 74, 101, and 128. The results reported in Bulletin No. 51 can not be computed directly in this way because the ration included a small fixed amount of linseed meal.

Omitting the results of the year 1904, which are obviously too high both as regards the maintenance requirement and the percentage availability, we obtain the following averages in round numbers:

	Available energy.	Metabolizable energy.
	Therms.	*Therms.*
Per 500 kilograms live weight	6.52	11.63
Per 1,000 pounds live weight	6.11	10.90

The variations from these averages which occur in individual cases illustrate the fact, already pointed out, that the economic as distinguished from the physiological requirement may vary considerably with different animals and under different conditions.

The experiments just cited are the only ones thus far reported in which this precise method of determining the maintenance requirement in terms of available energy has been followed. In the majority of investigations the effort has been to feed as nearly an exact maintenance ration as possible, making a correction for the small gains or losses by the animals, and the results of these experiments have usually been expressed in terms of metabolizable energy.

By far the most exact and satisfactory experiments of this sort, as well as the earliest, are those reported by Kellner from the Moeckern Experiment Station[1] in 1894 and 1896, in which the gain or loss of protein and fat (nitrogen and carbon balances) was determined by means of a Pettenkofer respiration apparatus. In these experiments the feed consisted exclusively of coarse fodder, viz, meadow hay, or, in two instances, a mixture of clover hay and oat straw. In six cases out of the eight the respiration experiments showed a small gain of protein and fat by the animal; that is, the ration was somewhat above the maintenance requirement. For example, the gains by ox A on meadow hay and the computed equivalent amounts of energy were:

	Material gained.	Equivalent energy.
	Grams.	*Therms.*
Protein	37.2	0.211
Fat	140.8	1.338
Total		1.549

In later investigations by Kellner, out of 100 units of metabolizable energy of meadow hay supplied in excess of the maintenance requirement, only 43 were recovered in the protein and fat gained by the body. To produce the gain observed in this experiment, therefore, may be computed to have required $1.549 \div 0.43 = 3.602$ therms of metabolizable energy and the ration must have contained this amount in excess of the maintenance ration. The following calcu-

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[1] Die Landwirtschaftlichen Versuchs-Stationen, vol. 44, p. 370; vol. 47, p. 310; vol. 53, pp. 6–16.

lation, therefore, shows the amount of metabolizable energy of meadow hay which was necessary for the maintenance of the animal:

		Therms.
Energy of feed		32.177
Energy of feces	11.750	
Energy of urin	1.945	
Energy of methane	2.114	
Energy of total excreta		15.809
Metabolizable energy of ration		16.368
Metabolizable energy equivalent to gain		3.602
Metabolizable energy for maintenance		12.766

This method of computing the metabolizable energy necessary for maintenance is obviously the same in principle as that employed in Armsby and Fries's experiments, differing only in the fact that the comparison is made on amounts of feed exceeding the maintenance ration. Kellner's results, however, can not be made the basis of a direct computation of the available energy required for maintenance, since it appears probable that a larger percentage of the energy of hay is available below the point of maintenance than is utilized for gain above it.[1]

In two cases (ox B and ox IV) the rations were less than the maintenance ration and the animals lost more or less protein and fat. In computing these experiments Kellner, in accordance with the ideas then generally accepted, simply added the energy equivalent to the loss of tissue to the total metabolizable energy of the feed to obtain the maintenance ration. It is evident, however, from what has subsequently been learned regarding the availability of metabolizable energy, as outlined in the foregoing paragraphs, that if, for example, ox B lost tissue equivalent to 1.498 therms it would have required more than this amount of metabolizable energy in the food to make good the loss, the quantity necessary depending upon the availability of the energy. Of the latter we have no determinations for this particular ration, but for purposes of computing a correction we may, perhaps, assume it to be the same as that found by Armsby and Fries for timothy hay, viz, about 57 per cent. On this assumption the equivalent amount of metabolizable energy which would have had to be supplied to reach the maintenance ration of ox B would have been $1.498 \div 0.57 = 2.628$ therms, a difference of 1.130 therms. For ox IV the corresponding correction is only 0.740 therm.

Making these slight changes in Kellner's original figures for these two animals for the sake of uniformity, his results are as follows:

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[1] Compare Bulletin 128, Bureau of Animal Industry, p. 59.

Maintenance rations of oxen—Kellner.

	Live weight.	Stable temperature.	Maintenance ration (metabolizable energy).		
			Per head.	Per 500 kilograms.	Per 1,000 pounds.
Thin animals:	*Kilos.*	° *C.*	*Therms.*	*Therms.*	*Therms.*
Ox V	602.1	14.7	11.675	10.316	9.668
Ox B	611.5	15.9	17.966	15.709	14.721
Ox A	619.8	15.9	12.766	11.060	10.365
Ox IV	622.8	14.9	15.861	13.701	12.840
Ox III	632.1	14.7	13.284	11.352	10.639
Ox II	632.4	15.0	14.457	12.362	11.585
Ox VI	644.0	14.8	11.771	9.944	9.320
Ox XX	671.7	16.5	15.213	12.486	11.702
Average			14.124	12.116	11.355
Average, omitting ox B			13.575	11.603	10.874
Fat animals:					
Ox 1	748.0	15.9	23.449	17.93	16.80
Ox B	750.0	15.2	19.385	14.79	13.86
Ox 3	858.0	16.1	22.162	15.46	14.49
Average			21.656	16.06	15.05

The observed maintenance ration of ox B is notably larger than that of the other animals. This animal refused to lie down during the respiration experiments and presumably, therefore, the result obtained with it is abnormally high.

Omitting this result, the maximum, minimum, and average maintenance rations per 1,000 pounds live weight were:

Metabolizable energy required for maintenance of cattle per 1,000 pounds live weight—Kellner.

	Per 1,000 pounds live weight.
Thin animals:	*Therms.*
Maximum	12.84
Minimum	9.32
Average	10.87
Fat animals:	
Maximum	16.80
Minimum	13.86
Average	15.05

If we are justified in assuming, on the basis of Armsby and Fries's results, that approximately 57 per cent of the metabolizable energy of these rations was available, then the foregoing amounts of metabolizable energy are equivalent to the following amounts of available energy:

Computed available energy required for maintenance of cattle—Kellner.

	Per 1.000 pounds live weight.	Per 500 kilograms live weight.
For thin animals:	*Therms.*	*Therms.*
Maxinum	7.32	7.81
Minimum	5.31	5.67
Average	6.20	6.61
For fat animals:		
Maximum	9.58	10.22
Minimum	7.75	8.42
Average	8.58	9.15

Both the averages and the range of the results obtained by Kellner and by Armsby and Fries for thin cattle on coarse fodder show a remarkably close agreement. The results upon fat cattle will be considered on subsequent pages.

In addition to the respiration experiments just considered, a number of live-weight experiments upon the maintenance ration of cattle have been reported.

Such trials were made by the writer at the Pennsylvania Experiment Station[1] in 1892 to 1897, the feed being either chiefly or entirely coarse fodder. The live weight was taken daily during relatively long periods and the nitrogen balance was also determined, and from these data an approximate computation of the loss of fat was attempted. The amount of methane excreted, and the corresponding loss of metabolizable energy, was calculated from the total carbohydrates digested. Computing the final results on the same assumptions as in the Moeckern experiments,[2] the results of 4 experiments each on 3 animals weighing from 400 to 500 kilograms, computed per 500 kilograms live weight, were:

Metabolizable energy in maintenance rations of steers—Armsby.

Ration.	Per 500 kilograms live weight.		
	Steer 1.	Steer 2.	Steer 3.
Chiefly or entirely coarse fodder:	*Therms.*	*Therms.*	*Therms.*
Experiment I, 1892–93	14.23	[17.09]	13.69
Experiment II, 1892–1894	13.61	13.56	12.40
Experiment VI, 1894–95	12.92	12.87	12.73
Experiment VII, 1894–95	13.03	12.76	[17.77]
Averages (omitting results in brackets)	13.45	13.06	12.94
Largely grain:			
Experiment VIII	11.72	9.15	10.70

Assuming, as before, that about 57 per cent of the metabolizable energy was available, and omitting the two apparently exceptional results, the maximum, minimum, and average results are:

Ration.	Metabolizable energy.		Available energy.	
	Per 500 kilograms live weight.	Per 1,000 pounds live weight.	Per 500 kilograms live weight.	Per 1,000 pounds live weight.
Coarse fodders:	*Therms.*	*Therms.*	*Therms.*	*Therms.*
Maximum	14.23	13.34	8.11	7.60
Minimum	12.40	11.62	7.07	6.62
Average	13.15	12.32	7.50	7.02
Largely grain	10.52	9.86	6.00	5.62

The results on coarse fodders are materially higher than those of the respiration experiments just cited, but the method is, of course, much less accurate.

Haecker[3] reports determinations of the maintenance rations of dry cows made in three successive years and in which three different animals were used. In these experiments the nutrients digested were determined directly and the sufficiency of the ration judged of from the live weight and appearance of the animals. Results obtained by Kellner[4] and by Armsby and Fries[5] show that

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[1] Pennsylvania Experiment Station, Bulletin 42.

[2] This differs somewhat from the method of computation followed in the original report of the experiments.

[3] Minnesota Experiment Station, Bulletin 79.

[4] Die Landwirtschaftlichen Versuchs-Stationen, vol. 53, pp. 440–445.

[5] Bureau of Animal Industry, Bulletins 51, 74, 101, and 128.

the metabolizable energy does not vary greatly from 1.6 therms per pound (3.5 therms per kilogram) of total digestible organic matter, even in rations differing widely as to the kinds of feed used. From the data regarding the digestible matter of the rations, therefore, the equivalent amounts of metabolizable energy may be estimated on this basis. Computing the results per 1,000 pounds in proportion to the two-thirds power of the live weight, instead of directly as does Haecker, the results are as follows:

Maintenance rations of dry cows—Haecker.

Cow.	Year.	Average live weight.	Average daily gain in live weight.	Kind of feed.	Metabolizable energy.	
					Per head.	Per 1,000 pounds live weight.
		Pounds.	*Pound.*		*Therms.*	*Therms.*
Alice	1896–97	808	0	Corn fodder	7.92	9.13
Belle	1896–97	1,010	0		9.26	9.19
Average						9.16
Belle	1897–98	1,072	0.27	Corn fodder, beets, and oil meal.	10.16	9.71
Lottie	1897–98	706	.27		7.01	8.83
Lottie	1898–99	757	.16	Not stated	8.96	10.75
Average						9.76
Average of all						9.51

In the first year's experiments the amount of digestible protein fed was small and the condition and appearance of the animals were not satisfactory. In the second and third years the rations were richer in protein, a slight gain in live weight was made, and the condition of the animals was entirely satisfactory at the close of the experiment. Since some gain was made in the second and third years the amount consumed was naturally somewhat larger than the first year. The proportion of grain to coarse fodder in the rations is not stated, but the results of the digestion trials indicate that it must have been small. If we assume 60 per cent availability, the computed available energy of the rations per 1,000 pounds live weight is:

	Therms.
Maximum	6.45
Minimum	5.30
Average of all	5.71

The results as thus computed run materially lower than those obtained at Moeckern and at the Pennsylvania station, in spite of the fact of a gain in live weight.

Evvard[1] fed three yearling steers for 60 days and one for 362 days on rations so adjusted and varied as to very exactly maintain their live weight, the average daily gain or loss being practically negligible. The experiment in the case of the first three animals followed a 30-day period in which a submaintenance ration was fed and the animals were therefore only in medium condition.[2]

The rations fed differed from those of the experiments previously quoted in containing a much larger proportion of grain, consisting of 4 parts by weight of alfalfa hay and 10 parts of mixed grain.[3] Evvard computes the available

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[1] Thesis for degree of M. S., University of Missouri, 1909.

[2] The animals graded in the maintenance period as follows: No. 500, common; No. 598, common; No. 596, good to medium; No. 595, medium.

[3] Eight-ninths corn chop and one-ninth old process linseed meal.

energy of the rations consumed from the data given in Bulletin 71 of the Pennsylvania station with the following results:

Maintenance rations of yearling steers—Evvard. (First experiment.)

No. of animal.	Length of experiment.	Average live weight.	Estimated available energy per day.	
			Per head.	Per 1,000 pounds[1] live weight.
	Days.	*Pounds.*	*Therms.*	*Therms.*
590	60	608	5.63	7.85
598	60	461	3.85	6.45
596	60	464	4.34	7.25
595	362	609	5.83	8.09

[1] Computed in proportion to the two-thirds power of the live weight.

In addition to the uncertainty attaching to such live-weight experiments, as well as to the fact that the available energy was estimated, there is also a special difficulty in determining the true maintenance requirement of growing animals, which will be referred to later. Nevertheless, the results appear to agree fairly well with those obtained in the respiration calorimeter experiments.

The metabolizable energy of the rations, also computed from the data given in Bulletin 71 of the Pennsylvania station, is, on the other hand, lower than that found in either the Pennsylvania or the Moeckern experiments, although agreeing well with Haecker's results on dry cows, viz, per 1,000 pounds live weight:

	Therms.
No. 590	10.42
No. 598	8.57
No. 596	9.63
Average	9.54

Evvard's first three animals were also fed a maintenance ration of the same feeds in the same proportions for 120 days after having been previously fed heavier rations for 127 days, during which No. 590 received about one-fourth of full feed, No. 598 about one-half, and No. 596 full feed. The results of this second maintenance period are summarized in the following table:

Maintenance rations of yearling steers—Evvard. (Second experiment.)

No. of animal.	Length of experiment.	Average live weight.	Estimated available energy per day.	
			Per head.	Per 1,000 pounds live weight.[1]
	Days.	*Pounds.*	*Therms.*	*Therms.*
590	120	706	6.47	8.15
598	120	665	6.44	8.45
596	120	860	9.66	10.62

[1] Computed in proportion to the two-thirds power of the live weight.

The data contained in the foregoing pages may be summarized in the following table showing the maximum, minimum, and average maintenance rations in various experiments. Armsby and Fries's results, as already noted, have been corrected to 12 hours standing. No statement of the amount of time passed standing and lying, respectively, is given in the reports of the other experiments.

Daily maintenance rations of cattle per 1,000 pounds live weight.

Investigators.	Condition of animals.	Number of animals.	Number of single trials.	Metabolizable energy.			Available energy.		
				Maximum.	Minimum.	Average.	Maximum.	Minimum.	Average
				Therms.	*Therms.*	*Therms.*	*Therms.*	*Therms.*	*Therms.*
Armsby and Fries..	Thin.......	3	7	12.78	8.52	10.90	7.06	4.86	6.11
Kellner.............	.....do.....	7	7	12.84	9.32	10.87	7.32	5.31	6.20
Do.	Fat........	3	3	16.80	13.86	15.05	9.58	7.75	8.58
Armsby (coarse fodder).	Thin.......	3	10	13.34	11.62	12.32	7.60	6.62	7.02
Armsby (much grain).	.....do.....	3	3	10.98	8.57	9.86	6.26	4.88	5.62
Haecker.............	.....do.....	3	5	10.75	8.83	9.51	6.45	5.30	5.71
Evvard, 60-day experiment.	.....do.....	3	3	10.42	8.57	9.54	7.85	6.45	7.18
Evvard, 362-day experiment.	.....do.....	1	1	....	....	10.74	....	....	8.09
Evvard, second experiment.	Partly fattened.	3	3	....	....	....	10.62	8.15	9.07
Average of all experiments.	Thin.......	*20*	*36*	*13.34*	*8.52*	*10.50*	*7.85*	*4.86*	*6.31*
	Fat........	*6*	*6*	....	....	*15.05*	....	....	*8.83*
Average of respiration experiments.	Thin.......	*10*	*14*	*12.84*	*8.52*	*10.89*	*7.32*	*4.86*	*6.16*

The foregoing results justify the statement that the maintenance ration of thin cattle, expressed in terms of available energy, ranges in general from 5 to 7.5 therms per 1,000 pounds live weight, averaging a little above 6 therms. The maintenance ration of fat animals appears to be distinctly greater than that of thin ones.

It should be noted that the term available energy is used in the sense defined on pages 20–22, as determined by a comparison of experiments upon submaintenance rations. This available energy is not necessarily identical with the energy values in terms of which the values of feeding stuffs and the requirements of animals have been expressed by Kellner and others (compare Farmers' Bulletin 346), since his results were obtained by a comparison of supermaintenance (productive) rations. Such scanty data as are now on record seem to indicate that the two are substantially the same in case of concentrated feeds, but that the available energy of coarse feeds below maintenance may be greater than their productive values above the point of maintenance. If this should prove to be the case, then evidently an estimated requirement of 6 therms of Kellner's production values will give a maintenance ration ample for practical purposes, but which will be a somewhat too large deduction to make in estimating the productive part of the ration.

SHEEP.

Data regarding the maintenance rations of sheep are less complete than for those of cattle. No experiments are on record in which the requirement of available energy has been directly determined, and but few respiration experiments have been made. Most of the recorded data are based upon live-weight experiments.

In 1867–68 Henneberg and his associates[1] conducted a series of respiration experiments upon two mature sheep receiving approximately a maintenance ration of meadow hay. Two digestion experiments, including determinations of the nitrogen balance, were made with each of the animals. During each of these digestion experiments three respiration experiments were made upon the two animals together. The results of these determinations vary so little that their average is sufficient for our present purpose. Estimating, as in some of the experiments on cattle, that each kilogram of digestible organic matter contains approximately 3.5 therms of metabolizable energy, and further, that, as in the case of Kellner's steers, 43 per cent of the metabolizable energy of the feed could be stored up in the form of gain of flesh and fat, the following computation per day and head may be made:

Maintenance ration of sheep—Henneberg and Stohmann.

Live weight, exclusive of wool	kilograms		45.4
Digestible organic matter per day	grams		539.1
Gain by animal:			
Protein	do		7.95
Fat	do		13.75
			Therms.
Metabolizable energy of ration 0.5391×3.5			1.887
Metabolizable energy equivalent to gain:		Therm.	
Protein, 0.00795 kilo.×5.7		0.0453	
Fat, 0.01375 kilo.×9.5		.1306	
		.1759 ÷0.43	.409
Metabolizable energy for maintenance			1.478

The foregoing ration is equivalent to 1.574 therms per 50 kilograms, or 1.475 therms per 100 pounds, computed in proportion to the two-thirds power of the live weight.

In 1872 Henneberg, Fleischer, and Müller[2] began a series of respiration experiments upon sheep in which wheat gluten was added to a basal ration of hay and ground barley. The basal ration of the first period proved to be but slightly greater than the maintenance ration. Making the same calculations as before, but assuming that 50 per cent of the metabolizable energy of the ration might serve for the production of gain, since a portion of the ration consisted of grain, we have the following:

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[1] Neue Beiträge, etc., pp. 68–286.

[2] Jahresbericht der Agriculturchemie, vol. 16–17, II, 145.

Maintenance ration of sheep—Henneberg, Fleischer, and Müller.

Live weight	kilograms	34.20
Digestible organic matter per day	grams	562.94
Gain by animal:		
Protein	grams	1.94
Fat	grams	43.60

		Therms.
Metabolizable energy of ration 0.56294×3.5		1.970
Metabolizable energy equivalent to gain—		
	Therm.	
Protein, 0.00194×5.7	0.01106	
Fat, 0.0436×9.5	.41420	
	.42526 ÷ 0.50	.851
Metabolizable energy for maintenance		1.119

This result is equivalent to 1.441 therms per 50 kilograms or 1.350 therms per 100 pounds live weight.

Hagemann,[1] from the results of a digestion and metabolism experiment and of 42 short[2] respiration periods with the Zuntz type of apparatus on a mature sheep averaging 50.33 kilograms live weight, computes an approximate energy balance which may be put in the following form, assuming that 50 per cent of the surplus metabolizable energy of the mixed ration might be recovered as gain:

Maintenance ration of sheep—Hagemann.

		Income.	Outgo.
Feed:		*Therms.*	*Therms.*
Alfalfa hay		2.181	
Corn meal		1.524	
Uneaten			0.009
Excreta:			
Feces			1.332
Urine			.146
Gain:	*Therm.*		
1.44 grams protein	0.008		
46.20 grams fat	.439		
	.447 ÷ 0.50		.914
Maintenance			1.304
		3.705	3.705

In addition to the foregoing experiments there are a number of digestion experiments by Wolff, in which the live weight of the animals was approximately maintained. In 1871[3] two series of experiments were made upon the relative digestive power of three breeds of sheep for an approximate maintenance ration. A comparison of the live weights of the animals is possible only for the second series, in which the ration consisted of clover hay and potatoes. The total organic matter digested per day and head and the average live weights at the beginning and end of the experiment were as given in the

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[1] Archiv für (Anatomie und) Physiologie, 1899, Suppl., p. 138.

[2] Usually not exceeding 30 to 40 minutes.

[3] Landwirtschaftliche Jahrbücher, vol. 1, p. 533.

table, which also shows the metabolizable energy equivalent to the digested organic matter (3.5 therms per kilogram), both per head and per 50 kilograms live weight, computed in proportion to the two-thirds power of the latter. The average result is equivalent to 1.634 therms per 100 pounds live weight.

Maintenance rations of sheep—Wolff.

Breed.	Number of animals.	Live weight.[1]		Digested organic matter per day and head.	Equivalent metabolizable energy per day.	
		Initial.	Final.		Per head.	Per 50 kilograms live weight.
		Kilos.	*Kilos.*	*Grams.*	*Therms.*	*Therms.*
Electoral merino	1	39.85	39.20	345.35	1.209	1.414
	2	42.05	40.50	342.34	1.198	1.361
Natives	3	49.85	49.50	537.97	1.883	1.891
	4	47.45	47.20	523.24	1.831	1.898
Southdowns	5	67.55	66.20	680.43	2.382	1.963
	6	59.05	59.70	620.38	2.171	1.936
Average					1.779	1.744

[1] Average of 5 or 6 consecutive days.

In 1892–93 Wolff[1] made a series of experiments with sheep on the influence of salt upon digestibility. In the first two periods of this series an approximate maintenance ration of 1,000 grams of meadow hay per day and head was fed. Since the salt was found not to affect the digestibility of the feed, we may use the results of the two periods as a basis for computing the maintenance ration. The average live weights per head were as follows:

	January 2, 3, and 4.	February 5, 6, and 7.
Sheep No. 1	42.9	44.0
Sheep No. 2	43.8	42.8
Sheep No. 3	42.8	44.5
Sheep No. 4	42.2	42.0
Average	42.9	43.3

The feed consumption was uniform with all the animals and the percentage digestibility showed but very slight variations, so that we may regard the average of the eight trials as representing approximately the maintenance ration. The average amount of organic matter digested per day and head was 476.28 grams. Reckoning, as before, 3.5 therms of metabolizable energy per kilogram, this corresponds to 1.667 therms per head, equivalent to 1.841 therms per 50 kilograms or 1.725 therms per 100 pounds live weight, computed in proportion to the two-thirds power of the latter.

Wolff[2] has also computed the digestible matter in the rations consumed by sheep in a number of the earlier experiments by Henneberg. The average of six rations which appeared amply sufficient for maintaining the live weight of the animal was, per head:

	Kilograms.
Live weight	40.05
Organic matter digested	.566
Equivalent metabolizable energy ......therms	1.981

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[1] Landwirtschaftliche Jahrbücher, vol. 25, p. 175.

[2] Ernährung der Landwirtschaftliche Nutztiere, pp. 416–419.

Computed in the usual way, this is equivalent to 2.300 therms per 50 kilograms. This is a much higher result than was obtained in any of the other experiments, and in view of the fact that the digestibility of the rations was estimated and that the feed was of a somewhat varied character it seems permissible to omit this result from consideration.

The results of the experiments cited, omitting the ones last mentioned, may be summarized as follows:

Daily maintenance rations of sheep.

Kind of experiment, and investigator.	Metabolizable energy.	
	Per 50 kilograms live weight.	Per 100 pounds live weight.
Respiration experiments:	*Therms.*	*Therms.*
Henneberg and Stohmann	1.574	1.475
Henneberg, Fleischer, and Müller	1.441	1.358
Hagemann	1.304	1.222
Average	1.440	1.352
Digestion experiments:		
Wolff, 1871, 6 experiments	1.744	1.634
Wolff, 1892-3, 8 experiments	1.841	1.725
Average	1.793	1.680
Average of all	1.581	1.483

It is of some interest to compare this average maintenance ration of sheep with the corresponding results for cattle. If we assume that the surfaces exposed by these two species are roughly proportional to the two-thirds powers of their live weights, the corresponding maintenance ration for a 1,000-pound steer would be $1.483\times\left(\frac{1000}{100}\right)^{\frac{2}{3}}=6.885$ therms of metabolizable energy as compared with an average of 10.50 therms for cattle. While such a comparison is, of course, but a rough approximation, it nevertheless seems to show conclusively that the metabolism of the sheep per unit of surface is distinctly lower than that of cattle. No obvious reason for such a difference suggests itself. That it can hardly be due to the direct effect of the wool in diminishing the radiation of heat will appear from a discussion, in a later section, of the influence of external temperature on the maintenance requirement.

SWINE.

Two determinations of the fasting katabolism of swine have been reported by Meissl, Strohmer, and Lorenz.[1] The experiments were made with the respiration apparatus, no calorimetric determinations being carried out.

Computing the energy katabolized by the use of Rubner's factors for the energy corresponding to the nitrogen and carbon excreted, the writer[2] obtained

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[1] Zeitschrift für Biologie, vol. 22, p. 63.

[2] Principles of Animal Nutrition, p. 452.

the figures contained in the third column of the following table. Kellner[1] has recomputed the results, using the exact figures for the carbon, nitrogen, and energy content of the flesh of swine which were obtained by Köhler, with the results shown in the last column.

Fasting katabolism of swine—Meissl, Strohmer, and Lorenz.

	Live weight.	Fasting katabolism.	
		Armsby.	Kellner.
	Kilos.	*Therms.*	*Therms.*
Experiment V	140	2.607	2.737
Experiment VI	120	2.291	2.385

Computing Kellner's figures to uniform live weight in proportion to the surface we have:

	Per 50 kilograms.	Per 100 pounds.
	Therms.	*Therms.*
Experiment V	1.377	1.290
Experiment VI	1.333	1.249
Average	1.355	1.270

These figures, according to the principles enunciated in the foregoing pages, may be regarded as representing the available energy required for maintenance. No other direct determinations of this requirement appear to have been made.

In addition to the foregoing, a number of live-weight experiments have been reported.

Dietrich[2] determined the amount of feed required by growing pigs to maintain their live weight at different stages of growth. The trials were made when the animals reached approximately the weights of 50, 100, 150, and 200 pounds, 4 animals being used. The digestibility of the ration fed at the weight of 150 pounds was also determined. The actual average amounts of feed required per day and head were as follows:

Maintenance rations of swine at different ages—Dietrich.

Period.	Average live weight.	Feed required for maintenance.		
		Corn meal.	Middlings.	Skim milk.
	Pounds.	*Pounds.*	*Pounds.*	*Pounds.*
I	49.62	0.15	0.15	1.2
II	98.75	.40	.40	1.6
III	151.25	.80	.80	1.6
IV	201.37	.67	1.33	....

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[1] Die Ernährung der Landwirtschaftliche Nutztiere, 5th ed., p. 156.

[2] Wisconsin Experiment Station, 16th Report, 1899, p. 31.

Assuming the composition of the feeding stuffs used to be fairly represented by the averages given in Farmers' Bulletin 22 (revised) and using Jordan's digestion coefficients for middlings, oil meal, and skim milk, and Kellner's coefficients for corn meal, the writer has computed the digestible nutrients contained in the rations consumed with the results shown in the following table. The metabolizable energy of the rations has been computed from the amount of digestible nutrients, using the factors—

	Calories per gram.
Digestible protein	4.1
Digestible nitrogen-free extract	4.2
Digestible crude fiber	3.5
Digestible ether extract	8.8

Computed digestible nutrients and metabolizable energy per day—Dietrich's experiments.

Period.	Digestible nutrients per head.			Metabolizable energy.		
	Protein.	Carbohydrates.	Fat.	Per head.	Per 50 kilograms live weight.	Per 100 pounds live weight.
	Pounds.	*Pounds.*	*Pounds.*	*Therms.*	*Therms.*	*Therms.*
I	0.065	0.241	0.012	0.628	1.069	1.002
II	.126	.561	.028	1.415	1.523	1.427
III	.204	1.038	.050	2.556	2.069	1.939
IV	.205	1.159	.057	2.817	1.885	1.766

Taylor[1] reports quite similar experiments with animals weighing respectively 50, 100, and 150 pounds. Computed in the same manner as the previous experiments, the results are as follows:

Maintenance rations of swine at different ages—Taylor.

Period.	Average live weight.	Feed required for maintenance.		
		Shorts.	Corn meal.	Oil meal.
	Pounds.	*Pounds.*	*Pounds.*	*Pounds.*
I	52.1	0.48	0.24	0.08
III	103.5	1.14	.57	.19
V	157.0	1.20	.60	.20

Computed digestible nutrients and metabolizable energy per day—Taylor's experiments.

Periods.	Digestible nutrients per head.			Metabolizable energy.		
	Protein.	Carbohydrates.	Fat.	Per head.	Per 50 kilograms live weight.	Per 100 pounds live weight.
	Pounds.	*Pounds.*	*Pounds.*	*Therms.*	*Therms.*	*Therms.*
I	0.096	0.434	0.025	1.105	1.821	1.707
III	.288	1.030	.058	2.618	2.730	2.558
V	.240	1.083	.061	2.753	2.174	2.037

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[1] Wisconsin Experiment Station Report, 1901, p. 67.

Carlyle[1] reports the average daily food for maintenance of 12 brood sows for eight weeks after weaning their pigs as follows:

	Pounds.
Average live weight	306
Feed per day and head:	
Corn	1.49
Shorts	1.49
Oil meal	.50
Skim milk	6.90

The computed digestible nutrients and energy of the above ration are:

	Pounds.
Digestible protein	0.654
Digestible carbohydrates	2.307
Digestible fat	.117
Equivalent metabolizable energy:	Therms.
Per head	6.079
Per 50 kilograms live weight	3.077
Per 100 pounds live weight	2.884

In a preliminary report of experiments upon pig feeding, Dietrich[2] estimates the maintenance ration of growing pigs per 100 pounds live weight to be:

	Pounds.
Digestible crude protein	0.10
Digestible carbohydrates	.40
Digestible fat	.04

This ration, using the same factors as before for the metabolizable energy, is equivalent to 1.181 therms per 50 kilograms or 1.107 therms per 100 pounds live weight.

The foregoing results show a wide range in the apparent food requirement for the maintenance of live weight. In general, the lower results seemed to have been reached with the younger animals. This may be due, however, to the fact that, as will be shown in a subsequent paragraph, the maintenance of live weight in a young animal is not necessarily synonymous with the maintenance of its store of potential energy. If we omit the results obtained with the 50-pound animals and also omit Dietrich's results at the Illinois Station, since his experiments seem to have been with comparatively young animals, we find the range of results to be as follows:

	Per 50 kilograms.	Per 100 pounds.
	Therms.	*Therms.*
Minimum	1.523	1.427
Maximum	3.077	2.884
Average	2.243	2.102

On the basis of respiration experiments by Meissl as discussed by Kellner,[3] four rations consisting of not dissimilar feeds showed

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[1] Wisconsin Experiment Station, Bulletin 104, p. 31.

[2] Illinois Experiment Station, Circular 126, p. 116.

[3] Die Ernährung der Landwirtschaftliche Nutztiere, 5th ed., p. 157.

an approximate average utilization of 74.5 per cent of the metabolizable energy supplied in excess of the fasting katabolism. If we may apply this percentage to the average of the foregoing results regarding maintenance, we may compute the average requirement of available energy to be 2.243×0.745=1.671 therms per 50 kilograms, or 1.566 therms per 100 pounds, a result not differing very widely from the figures computed on a previous page from the results of experiments on the fasting katabolism, but with a very wide range of variation in individual cases.

THE HORSE.

The maintenance ration of the horse has been the subject of investigation by Zuntz and Hagemann, Wolff, Müntz, and Grandeau and Le Clerc.

ZUNTZ AND HAGEMANN'S INVESTIGATIONS.

Upon the basis of the results regarding the availability of energy for the horse, which have been described on pages 22–25, Zuntz and Hagemann[1] compute the fasting katabolism of the horse by substantially the same method as that employed on pages 34–35 for cattle.

For this purpose, they use those rest experiments on horse III in which the feed consisted of oats, hay, and straw. From the results of the respiration experiments made within the first five hours after feeding, they compute the total energy katabolism per day in the manner indicated on page 22, and from this subtract the energy expended in the digestion of the feed (not including the work of mastication), computed as shown on page 23. The remainder, of course, is the katabolism due to internal work, together with any katabolism resulting from a possible demand for heat to maintain the body temperature. Their results may be tabulated as follows:

Computed fasting katabolism of horse per day and head—Zuntz and Hagemann's experiments.

	Live weight.	Energy katabolism.	Feed.			Work of digestion.	Fasting katabolism.	Fasting katabolism per square centimeter body surface.	Season.
			Oats.	Straw.	Hay.				
	Kilos.	*Therms.*	*Kilos.*	*Kilos.*	*Kilos.*	*Therms.*	*Therms.*	*Gram-calories.*	
Period *a*	428.1	12.541	6	1	7	8.403	4.138	80.7	Winter.
Period *b*	434.1	11.674	6	1	6	7.704	3.970	76.7	Summer.
Period *e*	450.4	12.364	6	1	6	7.704	4.660	87.9	Winter.
Period *f*	449.1	11.783	6	1	4.75	6.830	4.953	93.6	Summer.
Period *i*	440.1	11.893	6	1	6	7.704	4.189	80.2	Winter.
Period *n*	448.2	11.407	4.8	0	5.1	5.672	5.735	108.5	Summer.
Period *c*	442.2	12.450	0	0	10.5	7.340	5.110	97.6	Do.
Period No. 118*c*	434.6	11.021	4.8	0.8	1.88	4.122	6.899	133.3	Winter.

In the experiments with a standard ration of 6 kilograms of oats, 1 of straw, and 6 (or 7) of hay, the average computed fasting katabolism for the three winter periods is 4.329 therms, while in the

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[1] Loc. cit., pp. 283–284 and 425–426.

single summer period it reaches the minimum of 3.970 therms. Zuntz and Hagemann consider that the latter represents approximately the minimum requirement for internal work and regard the higher figures obtained in the winter experiments as indicating a stimulation of the heat production by the low temperature to which the animal was exposed. The notably higher results obtained with the lighter rations they ascribe to a similar cause, viz, that the heat arising from the work of digestion and from the necessary internal work (fasting katabolism) was insufficient to maintain the body temperature. Accordingly, they regard the differences shown in column 8 of the foregoing table as including in these cases not only the minimum necessary for internal work but also an expenditure for heat production. In other words, they consider that the critical temperature (compare p. 71) for the horse is high as compared with that for cattle, and the critical amount of food small (compare p. 73). Earlier experiments[1] upon another horse in which lighter rations were fed confirmed this conclusion.

On the average of the 8 most satisfactory experiments out of 12, the estimated total katabolism per day and head was 11.027 therms upon a ration consisting of 3.5 kilograms of oats, 0.5 of straw, and 2.5 of hay. Computed in the same manner as in the foregoing examples, the expenditure of energy in the digestion of this ration is equal to 3.782 therms, which leaves a remainder of 7.244 therms, equivalent to 140.3 gram-calories per square centimeter of surface. This is a higher figure than any of those contained in the foregoing table, although the total katabolism was not notably different. The authors conclude, therefore, that the small amount of heat liberated by the digestive work was compensated for by an increased katabolism of body tissue.

From a balance experiment on the same animal in the respiration apparatus of the Göttingen Experiment Station they also compute[2] the metabolizable energy required for maintenance by subtracting from the total nutrients digested the fat equivalent of the protein and fat gained by the animal. They thus reach a maintenance ration per 500 kilograms, live weight, of 3.265 grams digestible nutrients, equivalent to 12.93 therms. Their final conclusion (loc. cit., p. 426) is that their animal required per head at least 11 therms, or per 500 kilograms live weight 12.10 therms, of heat to maintain his body temperature. In other words, this is the minimum of metabolizable energy which must be supplied in a maintenance ration, since if less be present, even although the ration supplies the requisite amount of available energy, body tissue will still be katabolized for the production of the heat necessary to maintain the body temperature.

Computed to 1,000 pounds live weight in proportion to the two-thirds power of the latter, Zuntz and Hagemann's maintenance ration is:

	Therms.
Available energy for internal work	4.08
Additional required for heat production	7.80
Total metabolizable energy required	11.88

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[1] Landwirtschaftliche Jahrbücher, vol. 18, p. 1; vol. 27, Ergänzungs Band III, pp. 356–257.

[2] Ibid., p. 423–424.

The maintenance requirement as measured by the computed fasting katabolism is notably less than that of cattle. The same criticisms which have been made of Zuntz and Hagemann's conclusions as regards availability are also applicable, of course, to his computation of the maintenance requirement.

WOLFF'S INVESTIGATIONS.

Wolff has also determined by a different method the maintenance ration of the horse in the experiments whose results as regards the available energy of feeds have already been mentioned on page 25. As there noted, the amount of work performed by the horse was adjusted so as to be as nearly as possible in equilibrium with the feed consumed. Wolff's experiments were made with a sweep power arranged to serve also as a dynamometer. The actual measurements of the work performed, except in the later experiments, proved to be too low; but Wolff believes them to be relatively correct, so that the ratio between the work as measured and the additional feed required to produce it may still serve as the basis of computation.

In the experiments of 1877–1886[1] it was found that the work performed in 100 revolutions of the dynamometer required the addition to the ration of 315 grams of digestible nutrients. It is important to note, however, in view of what follows, that this additional digestible material included no digestible crude fiber—that is, that it was practically derived from the grain added in the periods of heavier work. Subtracting from the total digestible nutrients of the ration, therefore, an amount computed on this basis to be equivalent to the work done leaves a remainder representing the nutrients required for maintenance on the virtual assumption that all the work done was performed at the expense of nutrients derived from the grain. The results of these computations are summarized in the following table:

Maintenance rations of horses—Wolff, 1877–1886.

Animal.	Number of experiments.	Total nutrients.	Nutritive ratio.	Live weight.	Number of revolutions.	Equivalent nutrients.	Maintenance ration by difference.
		Grams.		*Kilos.*		*Grams.*	*Grams.*
Horse I	4	6,305.6	1:5.79	521	600	1,890	4,416
Horse II:							
1881–82	7	5,831.1	1:6.64	477	546	1,720	4,111
1882–83	4	6,748.3	1:6.37	486	662	2,085	4,663
1883–84	6	5,920.2	1:7.26	457	567	1,786	4,134
Average	17	6,078.4	1:6.80	473	577	1,818	4,260
Horse III:							
1881–82	6	5,313.8	1:7.16	454	404	1,273	4,041
1882–83	6	6,061.3	1:6.88	469	683	2,152	3,909
1883–84	5	5,734.8	1:7.55	473	580	1,827	3,908
1885	4	5,761.2	1:7.57	473	575	1,811	3,050
Average	21	5,717.8	1:7.29	467	501	1,766	3,952

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[1] Grundlagen für die rationelle Fütterung des Pferdes, 1886, 66–155; Neue Beiträge; Landwirtschaftliche Jahrbücher, vol. 16, Ergänzungs Band III, 1–48.

Computed to 500 kilograms live weight on the basis of what Wolff regards as the normal weights of the animals, the foregoing maintenance rations are:

	Grams.
Horse I	4,143
Horse II	4,260
Horse III	4,167

A series of similar experiments on horse III, weighing 475 kilograms, in 1885–86,[1] computed in substantially the same way, gave results for the maintenance ration agreeing well with those of earlier years, viz:

Maintenance rations of a horse—Wolff, 1885–86.

Period.	Per head.	Per 500 kilograms.
	Grams.	*Grams.*
I	3,934	4,141
II	3,984	4,194
III and V	4,001	4,212
VIIb	4,094	4,310
VIII	4,094	4,310
Average	4,021	4,232

In a succeeding period (IX), however, in which hay alone was fed, a decidedly higher result was obtained, viz, 4,357 grams per head, or 4,586 grams per 500 kilograms.

In these earlier experiments, in accordance with the views then prevalent, Wolff regarded the so-called nutrients as of equal value whatever their source. The experiment with hay, just mentioned, however, suggested that such was not the case and this suspicion was confirmed by later investigations which clearly showed the superiority of the digestible matter of grain over that of hay. This superiority was not apparent in the earlier experiments because the proportions of grain and coarse fodder were not widely different in the several experiments, the coarse fodder furnishing on the average fully one-half of the dry matter fed.

This difference, suggested by the experiment on hay, was demonstrated by a comparison by Wolff[2] of his own results with those obtained by Grandeau and Le Clerc[3] in experiments upon two cab horses receiving only a small amount of walking exercise. The ration used by the latter experimenters consisted of about 75 per cent of grain as against less than 50 per cent in Wolff's experiments, and from it Wolff computes an average maintenance ration per 500 kilograms of 3,626 grams of digestible nutrients as compared with the 4,000 to 4,200 grams of the foregoing table.

Direct experiments by Wolff[4] likewise show that the digestible nutrients of concentrated feed (oats) are more valuable for work production than those of coarse feed (hay). The experiments were made in the manner already described, the draft being uniformly 60 kilograms. Although the measurements of the work actually done are probably incorrect, it may be assumed to have been substantially proportional to the number of revolutions of the dynamometer. A ration of 3 kilograms of hay and 5.5 kilograms of oats served as the basal ration, to which was added on the one hand 4 kilograms of hay and

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[1] Landwirtschaftliche Jahrbücher, vol. 13, Ergänzungs Band III, p. 32.
[2] Ibid., pp. 73–81.
[3] L'Alimentation du Cheval de Trait, 1883, II, 86 and 131.
[4] Loc. cit., pp. 84–95.

on the other 1½ kilograms of oats. The nutrients digested in each case and the equivalent amounts of work secured were:

Nutrients equivalent to work—Wolff, 1886–87.

Period.	Ration.	Digested.					Equivalent work.
		Protein.	Crude fiber.	Nitrogen-free extract.	Ether extract.	Total (fat × 2.4).	
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Revolutions.*
I–III	7 kilograms hay, 5.5 kilograms oats	822.58	816.68	3,889.64	186.72	5,973.62	750
V	3 kilograms hay, 5.5 kilograms oats	626.46	422.74	3,068.78	184.78	4,561.13	350
	4 kilograms hay	196.12	393.94	821.18	1.94	1,412.49	400
	Per 100 revolutions					353.12	
VI	3 kilograms hay, 7 kilograms oats	754.52	355.24	3,719.24	252.17	5,434.21	700
V	3 kilograms hay, 5.5 kilograms oats	626.46	393.94	3,068.46	184.78	4,561.13	350
	1.5 kilograms oats	128.06	−67.50	650.78	67.39	873.08	350
	Per 100 revolutions					249.45	

The relative value of the digested matter of hay and of oats for work production in these trials was thus approximately as 5 : 7.

The digestible nutrients added to the ration by the oats in period VI included no crude fiber, and, as the table shows, 249 grams of these fiber-free nutrients were found equivalent to 100 revolutions of the dynamometer with a draft of 60 kilograms, which is practically equivalent to the 315 grams per 100 revolutions with 76 kilograms draft found in the earlier experiments (p. 57) in which also, as was noted, the additional nutrients were practically fiber-free. Of the digestible nutrients added to the ration in the form of hay in period I–III, on the other hand, over one-fourth consisted of crude fiber, and in this case 353 grams were found to be equivalent to 100 revolutions of the dynamometer. If, however, the digestible crude fiber be omitted in this case, it appears that the fiber-free nutrients of the hay were practically equivalent to those of the oats, 255 grams being required for each 100 revolutions.

As noted previously, Wolff recomputed his experiments on the assumption that the crude fiber was valueless, and obtained results expressed in terms of fiber-free nutrients which were consistent among themselves and agreed with those obtained by Grandeau. The following table contains a summary of the results obtained for the maintenance ration expressed both in terms of total nutrients (including digestible crude fiber) and of fiber-free nutrients:

Nutrients for maintenance per 500 kilograms live weight—Wolff.

Experiments.	Including fiber.	Fiber-free.
	Grams.	*Grams.*
Experiments of 1881–1885:		
Horse I	4,143	3,378
Horse II	4,260	3,282
Horse III	4,167	3,306
Average	4,190	3.322
Experiments of 1885–86—Horse III:		
Period I	4,141	3,442
Period II	4,194	3,353
Period III and V	4,212	3,413
Period VII	4,310	3,549
Period VIII	4,310	3,490
Period IX	[4,586]	3,335
Average	[1] 4,232	3,430

[1] Omitting period IX.

Nutrients for maintenance per 500 kilograms live weight—Wolff—Continued.

Experiments.	Including fiber.	Fiber-free.
	Grams.	*Grams.*
Grandeau's experiments:		
Horse II	3,636	3,324
Horse III	3,617	3,328
Average	3,626	3,326
Experiments of 1886–87:		
Period I–III	4,202	3,342
Period IV	4,150	3,429
Period V	3,792	3,329
Period VI	3,738	3,364
Average	3,971	3,366

The figures inclusive of the crude fiber, as computed by Wolff, evidently correspond approximately with the amounts of metabolizable energy contained in various mixed rations which were sufficient for maintenance. In the earlier experiments, and in those later ones in which approximately equal proportions of hay and grain were consumed, the amount is approximately 4,200 grams per 500 kilograms live weight, which, using Zuntz and Hagemann's factor of 3.96 calories per gram, is equal to 16,632 calories. In the later experiments, in which a larger proportion of grain was fed, the total nutrients required for maintenance ranged from 3,600 to 3,700 grams, equivalent to from 14,257 to 14,652 calories. In other words, the amount of metabolizable energy necessary for maintenance varied with the proportion of coarse fodder present, as would be expected from the results with cattle recorded on previous pages.

The maintenance ration in terms of metabolizable energy, as thus computed, is comparable with that estimated by Zuntz and Hagemann, in the manner explained on pages 55–56, from the total heat production of the animal. That Wolff's results are higher is probably due to the relatively larger proportion of crude fiber in his maintenance rations, since, as shown on page 57, the work is assumed by Wolff's method of calculation to have been done at the expense of the nutrients of the grain, and consequently the remaining portion of the ration, which is regarded as the maintenance portion, was relatively poorer in grain and richer in coarse fodder.

Zuntz and Hagemann[1] attempt to estimate the difference due to the latter fact. They average 31 of Wolff's experiments, divided into two groups, viz, those on light and on heavy work, correcting the actual amount of work done for the loss of live weight and likewise for what they regard as Wolff's error in his estimate of the energy expended in locomotion. They also correct Wolff's estimate

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[1] Loc. cit., pp. 420–424; Principles of Animal Nutrition, p. 546.

of the energy of the digested matter by the use of the factor 3.96 calories per gram instead of 4.1 calories per gram. Their comparison of the two groups gives them by difference 31 per cent as the proportion of the available energy of the digested nutrients which was recovered in the form of work, a percentage corresponding very closely to that found for the work of draft in their experiments, viz, 31.4. Upon this basis, they compute in each group the amount of nutrients required for the total work done and by subtraction the total digestible nutrients required for maintenance.

Their results for an animal weighing approximately 500 kilograms are as follows, the equivalent metabolizable energy being obtained by the use of Zuntz and Hagemann's factor of 3.96 calories per gram. The average does not differ materially from that computed directly from Wolff's later experiments.

	Total digestible nutrients.	Equivalent metabolizable energy.
	Grams.	*Therms.*
Periods of light work	3,776	14.95
Periods of heavy work	3,763	14.90
Average	3,770	14.93

This result they compare with that obtained by them in a balance experiment with a respiration apparatus from which, as noted on page 56, they compute a maintenance ration of 12.93 therms. Their ration, however, contained notably less crude fiber than did Wolff's rations, the differences being as shown in the following table, which includes also the equivalent digestive work, estimated by Zuntz and Hagemann at 2.65 calories per gram:

	Difference in crude fiber fed.	Equivalent digestive work.
	Grams.	*Therms.*
Periods of light work	974	2.58
Periods of heavy work	956	2.53
Average	965	2.56

Subtracting this amount from the average computed from Wolff's experiments leaves a remainder of 12.37 therms as the metabolizable energy which would have been necessary for maintenance had Wolff's rations contained no more crude fiber than Zuntz and Hagemann's.

Wolff's experiments afford no data for computing in terms of available energy the maintenance requirement in the sense in which this term is used by Zuntz and Hagemann and in the discussion of the maintenance requirements of cattle, on pages 33 to 35, viz, as equivalent to the necessary demand for internal work. Even if we follow Wolff in regarding the energy of the fiber-free nutrients as an approximate expression of the available energy, his computation of the fiber-free nutrients required for maintenance simply shows the amount of available energy (in this sense) present in a maintenance ration, but gives no indication of how much of this may have been consumed in simple heat production.

MÜNTZ'S EXPERIMENTS.

Müntz,[1] in 1878–79, attempted to determine the maintenance ration of the horse by a different method, viz, by starting with an insufficient ration and gradually increasing it until an equilibrium between food and live weight was secured. His experiments were made upon horses of the Paris Omnibus Co. whose work ration was known from previous experiments. Upon one-third of their regular working ration four horses lost in from one to one and a half months an average of 1.02 pounds per day and head. The ration was then increased to one-half of the work ration. Upon this nine horses, including the four used in the previous experiments, gained on the average 1.08 pounds per day and head. Upon decreasing the ration to five-twelfths of the work ration, six other horses gained 0.46 pound per day and head. The amount of total organic matter consumed by the animals is recorded. Estimating from this the total digestible nutrients and computing the metabolizable energy of the latter at the rate of 3.96 calories per gram, the last two rations afforded the following results:

Metabolizable energy in rations of horses—Müntz.

	Average gain in weight per day.	Average live weight.	Digestible nutrients.	Metabolizable energy.	
				Per head.	Per 1,000 pounds live weight.
	Kilos.	*Kilos.*	*Grams.*	*Therms.*	*Therms.*
One half of work ration	+0.49	545	4,102	16.24	14.37
Five-twelfths of work ration	+0.19	523	3,417	13.53	12.31

GRANDEAU AND LE CLERC'S RESULTS.

Grandeau and Le Clerc,[2] in addition to the experiments recorded in connection with Wolff's results, fed five cab horses a daily ration of 8 kilograms of hay during a total of 14 periods of a month each (1 to 5 periods for each animal), during each of which the digestibility of the ration was determined. The animals had only a small

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[1] Annales de l'Institut National Agronomique, Tome 3, 1878–79.

[2] L'Alimentation du Cheval de Trait, 1883, III.

amount of walking exercise daily. The following are the results of the several periods:

Metabolizable energy in rations of horses—Grandeau and Le Clerc.

	Total digestible nutrients.[1]	Equivalent metabolizable energy.	Average daily gain or loss of weight.	Average live weight.
Horse 30845 (No. 1):	*Grams.*	*Therms.*	*Kilos.*	*Kilos.*
January, 1884	2,895.3	11.467	−0.19	394.9
April, 1884	2,351.9	9.315	+0.47	379.2
August, 1884	2,795.5	11.071	+0.03	365.0
September, 1884	2,927.8	11.595	[2] −0.03	366.3
October, 1884	2,897.1	11.473	[2] 0.00	366.0
Average	2,773.5	10.983	+0.06	374.3
Horse 29475 (No. 2):				
November, 1883	3,041.4	12.045	+0.59	423.6
Horse 29466 (No. 2):				
May, 1884	2,470.2	9.784	+0.42	404.0
June, 1884	2,909.5	11.523	+0.13	407.1
July, 1884	2,692.8	10.663	+0.18	410.6
Average	2,690.8	10.656	+0.24	407.2
Horse 29407 (No. 3):				
December, 1883	3,062.1	12.128	−0.05	413.9
Horse 26925 (No. 3):				
March, 1884	2,726.8	10.799	+0.82	419.0
June, 1884	2,644.5	10.473	+0.27	384.3
July, 1884	2,719.4	10.770	0.00	387.7
August, 1884	2,837.9	11.238	−0.01	388.4
Average	2,732.2	10.820	+0.27	394.9

[1] Including fat ×2.4.
[2] Omitting last day of each month.

On the average of all the periods, the results per day and head were as follows:

Total digestible nutrients (fat×2.4)	grams	2,783.7
Equivalent metabolizable energy, at 3.96 calories per gram	therms	11.03
Daily gain in weight	kilograms	0.19
Average live weight	do	393.6

The foregoing ration, which was apparently somewhat more than a maintenance ration, is equivalent to 12.12 therms of metabolizable energy per 1,000 pounds live weight. This is materially less than was obtained in Wolff's experiments and about the same as that found by Zuntz and Hagemann for rations containing much grain.

TRUE MAINTENANCE AND LIVE-WEIGHT MAINTENANCE.

The maintenance of an animal in the strict scientific sense signifies the preservation of the store of matter and of potential energy contained in the body, and only a ration which effects this is really a maintenance ration. As has appeared in the foregoing pages, however, much of our recorded information regarding the maintenance ration is derived from experiments in which the sufficiency of the ration was judged of from its effect in maintaining the live weight of the animal. In experiments on mature animals extending over a considerable period of time, it is unlikely that any gross error is involved, especially if determinations of the nitrogen balance show the protein supply to be adequate. In short periods, on the other hand, and especially in experiments upon young animals, the live weight is a notoriously untrustworthy guide. The general reasons for this are familiar, but in young animals another very important factor enters into consideration. As is well known, the tendency to growth is one of the most marked characteristics of young animals. Waters[1] has shown that this impulse to increase of tissue is so marked that it may apparently take precedence over the demand for maintenance, so that an animal may continue to increase in size of skeleton for a considerable time even on a submaintenance ration.

Some 15 immature cattle were fed for considerable periods on rations just sufficient to maintain their live weight. Under these conditions the animals continued to grow in height, in depth of chest, and length of head. At the same time, however, there was an evident falling off in the amount of fat tissue, both as judged by the eye and as shown by the appearance and by the chemical composition of the carcass. Histological studies, too, showed a reduction in the size of the fat cells, and analysis of the adipose tissue showed a lower fat and higher water and protein content than in check animals. What occurred was evidently a consumption of body fat to supply energy, while at the same time an approximately equal weight of protein tissue was produced which, on account of the relatively low energy value of protein and of the relatively large amount of water accompanying it, represented a much smaller quantity of energy than did the fat tissue which disappeared. In other words, the rations were not really, but only apparently maintenance rations. It is perhaps hardly correct to say that in these experiments growth was maintained at the expense of the fat of the tissues. A more exact statement of the case would be that the increase of protein tissue and water masked the loss of fat. Presumably this effect would be less marked in more mature animals, in which the true maintenance and live-weight maintenance would doubtless approach each other closely when measured over long periods.

FACTORS AFFECTING THE ENERGY REQUIREMENT.

The results of the experiments upon farm animals reported on previous pages render it evident that the actual maintenance requirement, even when computed to a uniform weight or size, is more or

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[1] Society for the Promotion of Agricultural Science, Proceedings of 29th Annual Meeting, p. 71.

less variable. For example, in the case of cattle, for which the most extensive and accurate data are available, the range of the energy requirement per day and 1,000 pounds live weight for thin animals in those experiments which are apparently the most accurate is 4.9 to 7.3 therms available energy or 8.5 to 12.8 therms metabolizable energy. Several causes may be responsible for these variations.

MUSCULAR ACTIVITY.

In considering the factors of the fasting katabolism (p. 9), attention was called to the large share which the muscles, and especially the voluntary muscles, have in the heat production of the animal. Even in a state of the most complete rest possible, a very considerable share of the total katabolism takes place in these tissues, due, presumably, to the state of constant slight tension or "tonus" of the living muscle.

MINOR MUSCULAR MOTIONS.

It is rarely the case, however, that an animal, even when at rest in the ordinary sense, does not execute more or less motions of various parts of the body, all of which involve an expenditure of energy, and even apparently insignificant movements may materially increase the amount of metabolism.

Zuntz and Hagemann,[1] for example, report a respiration experiment upon a horse in which the uneasiness caused by the presence of a few flies in the chamber of the apparatus caused an increase of 10 per cent in the metabolism. Johansson[2] compared the excretion of carbon dioxid by a fasting man when simply lying in bed (awake) with that occurring when all the muscles were as perfectly relaxed as possible. The results per hour were:

Excretion of CO_2 by fasting man.

	Grams.
Lying in bed	24.94
Complete muscular relaxation	20.72

Benedict and Carpenter[3] have compared the metabolism of men during sleep with that of the same subjects lying quietly in bed immediately after waking. In the three cases which they regard as strictly comparable the increase in the heat production during the waking period ranged from 5.8 to 15.2 per cent, averaging 11.4 per cent.

If, then, these comparatively insignificant movements have such a striking effect upon the metabolism, it is evident that the amount of muscular activity must be an important factor in determining the

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[1] Landwirtschaftliche Jahrbücher, vol. 23, p. 161.

[2] Skandinavisches Archiv für Physiologie, vol. 8, p. 85.

[3] Carnegie Institution of Washington, Publication 126, p. 241.

relative maintenance requirements of two animals even though their minimum physiological requirements may be identical. In experiments of any considerable duration on normal animals, it is impossible to avoid more or less expenditure of energy in this incidental muscular work, while it is often a matter of difficulty to make the different periods of an experiment comparable in this respect.

LYING AND STANDING.

Furthermore, considerable muscular exertion is involved during the waking hours in maintaining the relative position of the different members of the body. This is notably true of the effort of standing. In experiments by Armsby and Fries[1] the heat radiated per minute by a steer while standing was found largely to exceed that given off while lying, the excess in 25 experiments ranging from 28.3 to 64.5 per cent, although there were indications that the amount of feed consumed was also a factor.

On the other hand Dahm,[2] working in Zuntz's laboratory and by his methods, found an increase of only 8 per cent in the respiratory excretion of CO_2 by a young bull when standing as compared with that when lying, but Zuntz[3] himself in earlier experiments on a dog observed differences similar to those found by Armsby and Fries for cattle, the average oxygen consumption per minute being while lying 174.3 c. c. and while standing 245.6 c. c., or an increase of 41 per cent. Benedict[4] observed an increase of from 13.3 to 18.8 per cent, or an average of 16.5 per cent, in the heat production of man when standing as compared with that observed when sitting quietly in a chair.

It is clear, then, that of two animals, one of which lies down for 12 hours and the other for 8 hours out of the 24, the former will, other things being equal, require less energy for maintenance. In the results regarding the maintenance ration thus far reported, with the exception of the Pennsylvania experiments, this factor has not been taken into account.

INDIVIDUALITY.

It appears quite probable that those differences between the maintenance requirements of different animals which are ascribed somewhat vaguely to " individuality " are due to a large extent to varying amounts of muscular activity. In general, the nervous, restless animal will have a higher maintenance requirement than the quiet, phlegmatic one. Thus the table on page 40 shows that Armsby and

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[1] Bureau of Animal Industry, Bulletins 51, 74, 101, and 128.

[2] Biochemische Zeitschrift, vol. 28, p. 494.

[3] Archiv für die gesammte Physiologie des Menschen und der Thiere (Pflüger), vol. 68, p. 191.

[4] Loc. cit., p. 244.

Fries's steer A had in every case a materially lower maintenance requirement than steer B, even when the results were corrected to an equal number of hours standing per day. Computed per 1,000 pounds live weight and corrected to 12 hours standing, the results for available energy were as follows:

Available energy required for maintenance—Armsby and Fries.

	Steer A.	Steer B.
	Therms.	*Therms.*
1905	6.23	7.06
1906	5.70	6.38
1907	4.86	6.50

Steer B was an animal of rather pronounced dairy type and of a nervous disposition, and in all probability his higher maintenance requirement is to be ascribed to this fact. There can be little doubt that temperament is an important factor in determining the maintenance requirement and that there may be a considerable range of individual differences in this respect.

Similarly, any conditions tending to affect the degree of muscular activity will also tend to affect the maintenance requirement. The steer confined in a stall, for example, is likely to take less muscular exercise and therefore to require a smaller amount for maintenance than one simply confined to a pen or an open yard. The animal comfortably bedded and thereby induced to spend much of his time in lying down will consume a smaller portion of his feed for maintenance than one kept under less comfortable conditions. Any sort of excitement is likely to cause increased muscular activity and correspondingly increased consumption of food for maintenance.

CONDITION.

The condition of an animal—that is, the amount of adipose tissue carried—seems to influence the maintenance ration, at least in the case of cattle. This point was first investigated by Kellner.[1] His average result for three fat cattle, as shown in the table on page 43, is considerably higher when computed to the same live weight—that is, per unit of surface—than that for the seven lean animals, viz:

Unfattened--- 10.87 therms metabolizable energy per 1,000 pounds live weight.
Fattened------ 15.05 therms metabolizable energy per 1,000 pounds live weight.

Only one animal, however, was common to the two groups, viz, steer B, the results on which were excluded from the average of the unfattened animals on the ground that it was abnormally high, since the animal never lay down during the experiments. Curiously

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[1] Die Landwirtschlichen Versuchs-Stationen, vol. 50, p. 245; vol. 53, p. 14.

enough, this animal showed the lowest maintenance ration of the three fattened animals and, moreover, one which is distinctly less per unit of computed surface than in the unfattened state, viz:

Unfattened	14.72 therms metabolizable energy per 1,000 pounds live weight.
Fattened	13.86 therms metabolizable energy per 1,000 pounds live weight.

No other respiration experiments upon the relative maintenance requirements of fattened and unfattened animals are on record. Evvard's live-weight results, however, as given in the table on page 47, appear to confirm Kellner's conclusion that the relative maintenance ration of fattened animals is greater than that of the same animals unfattened.

One obvious reason why the maintenance requirement should be greater in the former case is the presumably greater muscular effort expended in standing, due to the greater weight to be supported. Zuntz and Hagemann in experiments upon the horse carrying weight on its back found that this increase was proportional to the amount of weight added. The increase indicated by Kellner's averages, however, is greater than would be computed on this assumption, and the same is true of Evvard's fat animals, the difference becoming greater as the animals become fatter.

AGE.

The energy requirement of a young animal is naturally smaller per head than that of an older animal on account of the difference in size. Whether there is any difference in the relative requirements—that is, in the requirement computed to uniform weight or surface—is not altogether clear, few specific results on farm animals being on record. Evvard's results on yearlings, page 46, are somewhat higher than most of the results which have been obtained with mature cattle, although, of course, these figures do not refer to the same individuals at different ages. Armsby and Fries,[1] in a series of respiration calorimeter experiments upon the same two animals in three successive years, observed a progressive decrease in the maintenance requirement of yearlings, 2-year-olds, and 3-year-olds when corrected to a uniform number of hours standing and computed to equal external surface (that is, in proportion to the two-thirds power of the weight).

Somewhat extensive data are on record regarding the metabolism of man at different ages. A summary and discussion of these by Tigerstedt[2] seem to show clearly that, leaving out of account infants and very aged persons, the metabolism per unit of surface diminishes from youth to maturity. In view of the slow development of man, these results are comparable to such as might be obtained during the first 6 to 12 months of the life of ordinary domestic animals and for

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[1] Bureau of Animal Industry, Bulletin 128, p. 55.

[2] Nagel's Handbuch der Physiologie des Menschen, I, 469.

these ages we have few satisfactory determinations of the maintenance requirement. The results upon swine cited on previous pages seem, it is true, to indicate the contrary relation, viz, a lower relative maintenance requirement for young animals. These results, however, are based upon live-weight experiments and, as already noted, are possibly lower than the true maintenance ration.

If it be true that the maintenance rations of young animals are relatively greater than those of older ones, we may fairly presume it to be due to a considerable extent to the greater amount of muscular activity usually exhibited by young animals.

EXTERNAL TEMPERATURE.

Farm animals belong to that general class known as warm-blooded or homoiothermic animals, whose bodies maintain a nearly constant temperature during health, regardless of that of their surroundings unless the latter be extreme, in which case death soon results.

REGULATION OF BODY TEMPERATURE.

Obviously, the regulating mechanism which maintains a constant temperature in spite of variations in the heat production of the body and in the temperature of its surroundings must be very efficient and very exactly adjusted. The regulation is effected in general in two ways, which may be called, respectively, physical and chemical regulation.

The heat of an animal escapes from the surface of the body chiefly through the skin, but to some extent also through the air passages, being removed both by conduction, by radiation, and by the evaporation of water. A rise of external temperature tends to check the outflow of heat exactly as it would in the case of an inanimate body. This tendency is compensated by a nervous reflex, which allows the capillary blood vessels of the skin to enlarge so that more blood flows through them, thus tending to raise the temperature of the surface and increase the outflow of heat. This phenomenon is readily observed in the flush which follows exposure to high temperatures. This method of regulation is analogous to opening the windows of a room to cool it. If the external temperature continues to rise, perspiration appears, or in the case of animals that have no sweat glands, like the dog, a peculiar form of breathing sets in, and relatively large amounts of water are evaporated from the skin or from the tongue and the interior of the mouth and throat. In this way large quantities of heat are carried off as the latent heat of evaporation of water, somewhat as an overheated room may be cooled by sprinkling the floor. When the external temperature falls again, the process is reversed. Sensible perspiration decreases and the blood is diverted from the capillaries of the skin to the internal capillaries. If this happens too quickly, it may even lead to congestion of the latter. The process is analogous to the closing of the windows of a room as the weather grows colder.

There is evidently a limit to this method of regulation. If the windows are entirely closed nothing more can be effected in this manner, and if the weather continues to grow colder the fire in the room must be increased. So if the external demand for heat becomes so great as to exceed the limits of adjustment in the body more fuel material is katabolized—that is, more heat is produced. This was first demonstrated by Carl Voit, who obtained the following results for the excretion of carbon dioxid by a man at various temperatures:

Influence of external temperature on metabolism of man—Carl Voit.

Temperature.	Carbon dioxid.	Urinary nitrogen.	Temperature.	Carbon dioxid.	Urinary nitrogen.
° *C.*	*Grams.*	*Grams.*	° *C.*	*Grams.*	*Grams.*
4.4	210.7	4.23	23.7	164.8	3.40
6.5	206.0	4.05	24.2	166.5	3.34
9.0	192.0	4.20	26.7	160.0	3.97
14.3	155.1	3.81	30.0	170.6	....
16.2	158.3	4.00			

Later and more comprehensive experiments with animals by Rubner have given corresponding results. Thus with two guinea pigs the following figures were obtained in 24-hour experiments:[1]

Influence of external temperature on metabolism—Rubner.

Mature animal.			Young animal.		
Temperature of air.	Temperature of animal.	CO^2 per kilogram and hour.	Temperature of air.	Temperature of animal.	CO^2 per kilogram and hour.
° *C.*	° *C.*	*Grams.*	° *C.*	° *C.*	*Grams.*
0	37.0	2.905	0	38.7	4.500
11.1	37.2	2.151	10	38.6	3.433
20.8	37.4	1.766	20	38.6	2.283
25.7	37.0	1.540	30	38.7	1.778
30.3	37.7	1.317	35	39.2	2.266
34.9	38.2	1.273			
40.0	39.5	1.454			

A later experiment by Rubner[2] upon a dog, in which the heat production was measured by a calorimeter, gave the following results:

Temperature of air.	Heat production per kilogram.
° *C.*	*Calories.*
7.6	83.5
15.0	63.0
20.0	53.5
25.0	54.2
30.0	56.2

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[1] Biologische Gesetze, p. 13.

[2] Archiv für Hygiene, vol. 11, p. 285.

CRITICAL TEMPERATURE.

It is clear from the foregoing results that when the external temperature falls below a certain limit the heat production of the animal shows a marked increase. This point at which the physical regulation gives way to or begins to be supplemented by the chemical regulation has been called the "critical temperature" for the animal. Above this temperature the radiating capacity of the body surface is varied to meet the varying conditions; below it this method of regulation is largely exhausted, and therefore the heat production is varied to suit the needs. This latter so-called chemical regulation is probably effected largely in the muscles, either by visible motion or by increase in the muscular tonus, either of which involves an increased heat production. This has been clearly shown to be true of man and probably applies also to other animals. Above the critical temperature there appears to be a slight increase in the heat production with rising temperature, probably due to the additional energy required for the various processes of physical regulation.

Any conditions tending to facilitate the escape of heat from the body would obviously act like a fall of temperature. Wind, for example, by removing the layer of partially warmed air next to the skin, tends to remove the heat more rapidly from the body, so that the cold is felt more severely on a windy day, while, on the other hand, the effect of a high temperature is modified by wind. A high percentage humidity of the air on a warm day hinders the removal of heat by evaporation, so that a moist heat is more trying than a dry heat. Cold, moist air, on the other hand, facilitates the escape of heat from the body by increasing the conducting power of the clothing, hair, or fur, so that a damp cold is more severe than a dry cold. The direct rays of the sun may impart a considerable amount of heat to the body, thus moderating the effect of low temperature and, on the other hand, increasing that of high temperature.

FEED CONSUMPTION A SOURCE OF HEAT.

For the sake of simplicity, the foregoing paragraphs have dealt especially with the case of the fasting animal, neglecting one important source of heat, viz, the consumption of feed. As was shown on pages 19–28, the latter results in increasing the katabolism of the body, and whether this be considered the result of the work of digestion or simply designated as specific dynamic effect, the fact is established beyond question. This heat, however, once generated, while unavailable for the physiological processes of the body is just as useful as external heat for keeping it warm. In other words, the consumption of feed will tend to have the same effect as a rise of external temperature. This being the case, it is clear that at temperatures considerably below the critical temperature, all the metabolizable energy of the feed will be of use to the body. Part of it will be available for physiological uses as already explained, but the remainder, while not available in this sense will nevertheless be of use as a source of heat.

ISODYNAMIC REPLACEMENT.

It was upon his earlier experiments (published in 1883) made under substantially the conditions just indicated that Rubner based his famous law of isodynamic replacement of nutrients which has played a large part in the discussion of nutrition problems. This law may be briefly stated as follows: *In amounts less than a maintenance ration the nutrients replace each other or body tissue in inverse proportion to their metabolizable energy.* The quantities which thus replace each other are accordingly said to be isodynamic. It need scarcely be pointed out that the minimum of protein required for the maintenance of the nitrogenous tissues is not included under this law. Rubner was careful to limit the law to small amounts of food. In his earlier publications he stated that it holds only below the maintenance ration; somewhat later he asserted[1] that it obtains up to an excess of about 50 per cent over the maintenance requirement.

These results of Rubner's have passed into the literature of physiology and are still largely interpreted as representing the relative values of nutrients, while Rubner's factors for the metabolizable energy of nutrients have been extensively used in computing the energy values not only of human dietaries but of stock rations as well. Historically, Rubner's earlier investigations mark an epoch in the science of nutrition. While similar views had previously been advanced by others, Rubner appears to have been the first to investigate the subject experimentally. The conception that the replacement values of the nutrients could be measured by the relative contributions of energy which they make to the activities of the body was a contribution of the first order to the study of nutrition problems, but the exact form given it in these earlier experiments proves to have been but a partial expression of the truth, as Rubner's own later experiment, as well as those of others, have fully demonstrated. (Compare pp. 26–28.)

RELATION OF MAINTENANCE RATION TO CRITICAL TEMPERATURE.

When its surroundings are above the critical temperature, the animal is producing a surplus of heat as a consequence of its necessary physiological activities and disposes of it by the processes of

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[1] Biologische Gesetze, p. 20.

physical regulation already described. The heat produced is then in a sense an excretum, and under these conditions obviously the external temperature does not materially affect the maintenance ration. The latter, as already shown, is measured by the amount of available energy necessary to support the vital processes, i. e., by the total fasting katabolism.

Below the critical temperature, however, the conditions are different. At relatively low temperatures all the metabolizable energy of the feed is used directly or indirectly to keep the animal warm, and as the external temperature falls, either more feed must be given or more tissue burned to supply the additional heat required to maintain the body temperature.

FEED CONSUMPTION LOWERS THE CRITICAL TEMPERATURE.

Since feed consumption is itself a source of heat, the animal consuming feed can, other things being equal, withstand a lower temperature than when fasting, and the larger the amount of feed consumed the lower is the corresponding temperature. The matter may also be put in the reverse way. For any particular (low) temperature there is a certain amount of feed the digestion and assimilation of which will yield an amount of heat sufficient to supplement that derived from the fasting katabolism, so as to just maintain the body temperature. This particular external temperature, then, is the critical temperature for that amount and kind of feed, and, conversely, that particular ration may be called the critical amount of feed for the particular external temperature.

CRITICAL TEMPERATURE FOR FARM ANIMALS.

The critical temperature for farm animals has not been definitely determined. In the case of cattle and probably of sheep, however, it is apparently rather low for animals consuming an ordinary ration. Thus Armsby and Fries have found that at about 18° C. the ration of cattle can be reduced considerably below the maintenance requirement without any evidence of increased oxidation of tissue for the sake of heat production. In the case of fattening animals consuming heavy rations and therefore producing a large amount of heat as a result of digestive work, the critical temperature would be still lower and experiments upon such animals have shown that they may be exposed to comparatively low temperatures, as in an open shed or yard, without causing them to oxidize any more food material. As already stated (p. 56) the critical temperature for the horse appears to be relatively higher.

THE PROTEIN REQUIREMENT FOR MAINTENANCE.

PROTEIN KATABOLIZED DURING FASTING.[1]

It has already been shown on pages 11–12 that in the previously well-nourished fasting animal the katabolism of protein supplies but a small part of the total energy required for the support of the vital functions. As a preliminary to the consideration of the protein requirement, however, some further consideration of the protein katabolism during fasting is desirable.

INFLUENCE OF PREVIOUS FEED.

The classic experiments of Carl Voit upon fasting dogs showed that while the protein katabolism in the early days of fasting may vary widely according to the previous feed, it soon falls to a comparatively low level which is approximately the same for the individual animal whatever its amount upon the initial days. This behavior is well illustrated by the following results, all upon the same animal, which have been fully confirmed by numerous subsequent experiments.[2]

Protein katabolism of fasting dog—Voit.

	2,500 grams meat.	1,800 grams meat; 250 grams fat.	1,500 grams meat.	1,500 grams meat.	Bread.
Urinary nitrogen[3] per day:	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Last day of feeding	84.4	60.7	51.7	51.7	11.5
First day of fasting	28.1	17.5	13.9	12.4	9.1
Second day of fasting	11.6	10.9	8.5	8.7	7.3
Third day of fasting	8.9	7.8	8.2	7.3	7.0
Fourth day of fasting	8.1	6.9	7.0	7.0	6.2
Fifth day of fasting	5.7	5.9	6.6	6.9	5.9
Sixth day of fasting	6.2	6.0	6.1	6.0	6.1
Seventh day of fasting	5.8	5.6	5.6	6.0	....
Eighth day of fasting	4.7	....	6.0	5.6	....
Ninth day of fasting	....	....	....	5.6	....
Tenth day of fasting	....	....	....	5.3	....

FASTING KATABOLISM VARIABLE.

It is not true, however, as is sometimes loosely stated, that the protein katabolism of a fasting animal is a constant quantity. On the contrary, in the presence of an adequate amount of body fat, its amount tends to diminish with the progress of fasting. This fact appears more or less clearly in the foregoing experiments, while in later ones it is quite marked. For example, in the experiments by

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[1] Compare references on p. 8.

[2] Zeitschrift für Biologie, vol. 2, p. 307.

[3] Computed from Voit's figures for urea. In earlier experiments upon the protein metabolism the urea in the urine, as determined by Liebig's titration method, was commonly taken as the measure of protein katabolism. Later experience has shown that these results are not strictly accurate, but the amount of urea under such circumstances is so nearly proportional to the total urinary nitrogen that the results as given above are entirely adequate as an illustration of the point under discussion.

Benedict, cited on page 15 in illustration of the relative constancy of the energy katabolism, the total protein katabolism showed a distinct falling off, and the same is true in less degree when computed per kilogram weight. The total urinary nitrogen upon the several days of the experiment was:

Protein katabolism of fasting man—Benedict.

Days.	Urinary nitrogen.		Days.	Urinary nitrogen.	
	Total.	Per kilogram weight.		Total.	Per kilogram weight.
	Grams.	*Gram.*		*Grams.*	*Gram.*
1	12.24	0.206	5	10.87	0.191
2	12.45	.211	6	10.74	.190
3	13.02	.223	7	10.13	.181
4	11.63	.202			

E. and O. Freund[1] determined the daily nitrogen excretion of Succi, a professional faster, with the following results:

Protein katabolism of fasting man—E. and O. Freund.

Days.	Nitrogen.	Days.	Nitrogen.	Days.	Nitrogen.
	Grams.		*Grams.*		*Grams.*
1	17.0	8	9.74	15	5.05
2	11.2	9	10.05	16	4.32
3	10.55	10	7.12	17	5.4
4	10.8	11	6.23	18	3.6
5	11.19	12	6.84	19	5.7
6	11.01	13	5.14	20	3.3
7	8.79	14	4.66	21	2.82

A similar phenomenon was observed by Michaud in experiments on the relative value of proteins described on a subsequent page. A dog, after 44 days abstinence from protein (16 days without food followed by 28 on nonnitrogenous food), excreted daily 1.42 grams nitrogen. The same dog after prolonged feeding upon low protein rations, however, showed in a three-days fast an average daily excretion of only 0.95 grams nitrogen. On the other hand, however, as already pointed out, the fasting protein katabolism may show a very marked increase with the progress of fasting in the absence of a sufficient store of body fat. It appears, then, that in fasting the protein katabolism is much more variable in amount than the total katabolism, and this fact must be remembered in any discussion of the protein requirement.

THE MINIMUM OF PROTEIN.[2]

It is evident that the comparatively small amount of protein katabolized in the fasting animal so long as its store of fat is reasonably abundant is at least all that is absolutely essential to the vital

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[1] Cited by Lusk.

[2] For a more exhaustive discussion of the subjects of this and succeeding paragraphs, including references to the literature, compare the references on page 8, in particular Magnus-Levy, pp. 198–423; Tigerstedt, pp. 391–480; Lusk, Chapters IV and V.

processes, since the latter go on for a considerable time in a substantially normal manner. The question at once arises whether this fasting katabolism represents the amount of digestible protein which must be supplied in the feed in order to maintain the protein tissues of the body.

INFLUENCE OF NONNITROGENOUS MATERIALS.

In the first place, it is to be remarked that, as just shown, the protein katabolism during fasting is by no means a fixed and definite quantity, but may vary even in the same individual within quite wide limits both absolutely and as regards the proportion of the total energy requirement which is supplied by it. From the results cited on pages 12–13, it is evident that a most important factor influencing the fasting katabolism is the stock of fat in the body and that when the latter is reduced protein is katabolized for the sake of its energy. In other words, a lack of readily available nonnitrogenous material in the body tends to increase the protein katabolism above its minimum value. Evidently, then, in seeking to determine the minimum amount of protein required for maintenance, the food given should contain a liberal supply of nonnitrogenous nutrients to supply the necessary energy for the animal, since otherwise there is danger that the protein will be katabolized for this purpose, resulting in an apparent increase of the maintenance requirement.

RELATION TO FASTING KATABOLISM.

In the early experiments upon this subject, especially those of Voit, the full significance of this fact had not been recognized. His experiments, in which increasing amounts of protein alone were fed (compare p. 79), showed that protein equal to two and a half to three times the fasting katabolism was necessary to reach nitrogen equilibrium, and this result was generalized and passed current for a considerable time.

Munk[1] seems to have been the first to challenge this view and to claim not only that an amount of protein equal to that katabolized during fasting is adequate, but that with an abundant supply of nonnitrogenous material, especially carbohydrates, in the feed a notably smaller amount of protein is sufficient to maintain the nitrogen balance. Munk's experiments either include no comparison with the fasting katabolism of the same animal or a comparison not in all respects satisfactory, but they show clearly that nitrogen equilibrium was maintained on a supply of protein less than that usually found to be katabolized in similar fasting animals.

On the other hand, extensive experiments by Voit and Korkunoff[2] on dogs led these experimenters to an opposite conclusion. Starting with a ration deficient in protein but containing a very liberal supply of nonnitrogenous nutrients, the protein of the feed was gradually increased until an amount was

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[1] Virchow's Archiv für Pathologische Anatomie und Physiologie und für Klinische Medizin, vol. 101, p. 91; vol. 133, Supp.; vol. 132, p. 91. Archiv für (Anatomie und) Physiologie, 1896, p. 183.

[2] Zeitschrift für Biologie, vol. 32, p. 58

reached sufficient to produce equilibrium between the income and outgo of nitrogen. Two series of experiments were performed, in one of which the nonnitrogenous nutrients consisted chiefly of fat, and another in which they consisted of carbohydrates. Considering only those experiments in which the feed consumed was more than sufficient in amount to supply the estimated demand of the body for energy, it was found that when the nonnitrogenous nutrients consisted of fat the nitrogen (protein) of the feed had to be increased to approximately 130 per cent of the amount katabolized in fasting before nitrogen equilibrium was reached—that is, before the stock of body protein was maintained. When, however, the energy demands of the body were supplied by carbohydrates instead of fats, a supply of nitrogen (protein) in the feed equal to or even somewhat less than the amount katabolized in fasting sufficed to insure nitrogen equilibrium.[1] Cremer and Henderson,[2] in experiments on a dog with a ration estimated to supply the necessary energy for maintenance, were unable to maintain nitrogen equilibrium on even as small an amount as did Voit and Korkunoff.

In the case of man, on the other hand, numerous experiments seem to have demonstrated that an amount of feed protein notably less than the ordinary fasting katabolism is sufficient to maintain nitrogen equilibrium, although even in this case the comparison in nearly every case is with the average fasting katabolism and not with that of the individual under experiment. This average for man, however, has been well established by numerous experiments and seems not to vary widely for individuals, while in Benedict's experiments[3] upon nutrition after fasting a material diminution of the protein katabolism of the subject was observed on the second and third days. In every case the body lost protein, but in experiments 70 and 74 there was a storing up of energy.

Protein katabolism during and after fasting.[4]

	Experiments 69 and 70.	Experiments 71 and 72.	Experiments 73 and 74.	Experiments 75 and 76.
Fasting:	*Grams.*	*Grams.*	*Grams.*	*Grams.*
First day	60.5	35.0	61.7	73.4
Second day	85.6	66.2	71.8	74.7
Third day	90.2	78.6	69.2	78.1
Fourth day	77.8	64.4	62.3	69.8
Fifth day	....	....	59.9	65.2
Sixth day	....	....	....	64.4
Seventh day	....	....	....	60.8
Food after fasting:				
First day	78.24	63.96	64.44	61.02
Second day	59.04	....	49.50	42.90
Third day	60.90	....	40.68	46.92

Another factor which must be taken into consideration in fixing the minimum of protein is what may be called the time element. Rubner calls attention to the fact that if the protein of the ration is consumed at a single meal there may be for a time a surplus of protein or its digestive products in the system,

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[1] Voit and Korkunoff put a different interpretation upon their results, basing it upon the fact that a certain portion of the urinary nitrogen is derived from the nitrogenous extractives of the flesh metabolized in the body. Compare the account of their experiments in the writer's Principles of Animal Nutrition, pp. 135–139.

[2] Zeitschrift für Biologie, vol. 42, p. 612.

[3] Loc. cit., pp. 456 and 529.

[4] The odd-numbered experiments were the fasting experiments. The even-numbered are those in which food was given and which immediately followed the corresponding fasting experiments.

while at a subsequent period of the day there may be a deficiency which will be made good by a draft upon the proteins of the tissues.

For the purpose of this discussion, it is unnecessary to pursue further the somewhat complicated question of the absolute protein minimum and its relations to the fasting protein katabolism, especially in view of the fact that, as has been shown, the latter is itself more or less variable. It appears well established that on a diet containing an abundance of carbohydrates a supply of protein equivalent to the fasting protein katabolism is sufficient to meet the needs of the organism, while it is possible that a less amount will suffice. Fats appear to be distinctly less efficient than carbohydrates in keeping the protein katabolism at the minimum. Precisely why this is the case has not been fully made out, although Landergren[1] has advanced the explanation that a minimum of carbohydrates is essential to the chemical processes of metabolism and that when a sufficient amount is not supplied in the feed, protein is katabolized for the sake of producing carbohydrates, with the result that on a low protein diet nitrogen katabolism is increased. In any case, it is clear that the protein requirement upon a mixed ration sufficient in quantity is comparatively small.

EFFECT OF SURPLUS OF PROTEIN.

INCREASES PROTEIN KATABOLISM.

But while a relatively small quantity of digestible protein is sufficient, in the presence of an abundant supply of fuel material, to maintain the body in nitrogen equilibrium, an increase of the feed protein above this minimum does not result in any large or long-continued gain of protein tissue by the mature animal, but causes a corresponding increase in the protein katabolism, as is shown by the prompt increase in the amount of nitrogen excreted in the urine.

This fact was demonstrated more than 50 years ago by C. Voit, in collaboration at first with Bischoff[2] and later alone and with Pettenkofer,[3] in experiments on carnivorous animals, and almost innumerable subsequent investigations have shown that it is true not only of these animals, but of man and of herbivorous animals as well. The protein katabolism is determined chiefly by the supply of digestible protein in the feed, and the body comes quite promptly into equilibrium with any amount above the maintenance requirement which can be consumed, the nitrogen of the excreta substantially equaling that of the feed. This is well illustrated by the following selection from Bischoff and Voit's results upon a dog,[4] arranged in the order of the amount of protein eaten.

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[1] Jahresbericht über die Forschritte der Tier-Chemie, vol. 32, p. 685.

[2] Gesetze der Ernährung des Fleischfressers, 1860.

[3] Published chiefly in the Annalen der Chemie und Pharmacie and the Zeitschrift für Biologie. See also Voit: "Physiologie des Stoffwechsels," in Hermann's Handbuch der Physiologie.

[4] Voit's compilation, Zeitschrift für Biologie, vol. 3, p. 5.

Daily protein katabolism of dog—Bischoff and Voit.

Dates.	Meat eaten.	Nitrogen of feed.[1]	Nitrogen excreted in urine.[2]
	Grams.	*Grams.*	*Grams.*
Nov. 26 to 27, 1858	176	6.0	12.6
Nov. 24 to 25	300	10.2	14.9
May 1 to 4, 1864	480	16.3	16.3
Apr. 20 to June 1, 1863	500	17.0	18.7
Nov. 22 to 23, 1855	600	20.4	22.9
Feb. 13 to 17, 1865	800	27.2	26.1
Nov. 20 to 21, 1858	900	30.6	31.7
Apr. 14 to 20, 1863	1,000	34.0	35.9
Nov. 18 to 19, 1858	1,200	40.8	41.1
Apr. 1 to 14, 1863	1,500	51.0	49.5
Mar. 25 to Apr. 1, 1859	1,800	61.2	59.7
Apr. 5, 1858	1,900	64.6	64.9
June 21 to 29, 1863	2,000	68.0	67.2
Jan. 22 to 25, 1858	2,200	74.8	71.9
Dec. 5 to 7, 1858	2,500	85.0	80.7
Jan. 25, 1858	2,660	90.4	84.5

Moreover, what has been shown to be true of an exclusively protein diet is substantially true also of one containing liberal amounts of fats or carbohydrates. Thus in the following selection from Bischoff and Voit's experiments[1] bearing upon this point it is clear that, notwithstanding the presence of considerable amounts of fat in the feed, the protein katabolism, as measured by the urinary nitrogen, increased substantially in the same ratio as the protein supply.

Daily protein katabolism of dog—Bischoff and Voit.

Dates (inclusive).	Feed.		Nitrogen of feed.[2]	Urinary nitrogen.[3]
	Fat.	Lean meat.		
	Grams.	*Grams.*	*Grams.*	*Grams.*
Nov. 22 to Dec. 1, 1857	250	150	5.1	7.3
Dec. 2, 1857	250	250	8.5	8.9
Dec. 5, 1857, to Jan. 5, 1858	250	500	17.0	14.4
Jan. 9 to 11, 1858	250	1,000	34.0	28.3
Jan. 15 to 18, 1858	250	1,500	51.0	45.9
Apr. 1 to 7, 1859	250	1,800	61.2	56.4
Jan. 13 to 14, 1859	250	2,000	68.0	63.4

Carnivorous animals have been extensively used in the investigation of such questions as the foregoing, and others which are to be discussed later, largely because with them it is possible to employ a diet consisting of but one or two simple nutrients, but the main facts which have been brought out by such investigations have been shown to be true also of herbivorous animals. In the latter, as in the carnivora, the protein katabolism is determined chiefly by the supply of protein in the feed.

As early as 1852, eight years before the publication of Bischoff and Voit's inevstigations, Lawes and Gilbert,[4] in discussing the results of theri fattening experiments upon sheep and pigs, called attention to the very wide variations

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[1] Gesetze der Ernährung des Fleischfressers, 1860, pp. 97–115.

[2] Average of nitrogen of lean meat, 3.4 per cent.

[3] Computed from urea.

[4] Report British Association for the Advancement of Science, 1852, Rothamsted Memoirs, Vol. II.

in the amount of protein consumed, both per unit of weight and especially per unit of gain, and concluded that the apparent excess of protein in some cases must have served substantially for respiratory purposes.

Of the numerous later and more specific investigations on herbivora in which the nitrogen excretion has been determined, the following[1] may serve as an example. Two sheep were fed in periods 1 and 7 a basal ration of hay and barley meal. To this ration were added in the intermediate periods varying amounts of nearly pure protein in the form of conglutin (of lupins) or of flesh meal. A comparison of the nitrogen digested from the ration with the urinary nitrogen shows that the latter increased and diminished substantially parallel with the former.

Protein katabolism of sheep per day and head—Henneberg and Pfeiffer.

	Sheep I.		Sheep II.	
	Nitrogen digested.	Nitrogen in urine.	Nitrogen digested.	Nitrogen in urine.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Period 1	8.18	7.48	7.81	6.98
Period 2	17.86	16.82	17.72	16.37
Period 3	27.22	25.75	27.33	23.94
Period 4	36.99	32.71	37.07	32.09
Period 5	26.76	25.63	26.91	24.54
Period 6	17.62	16.64	16.94	15.99
Period 7	8.34	8.06	8.00	7.62

UTILIZATION OF PROTEIN LIMITED.

That the mere giving of protein food can not cause a large storing up of protein is indeed sufficiently obvious from daily experience. The muscles of the weakling can not be converted into those of the athlete by feeding him upon a meat diet, nor the small man increased in size by a very abundant protein supply. The protein tissues of the mature animal have reached their natural limit of size and consequently the capacity of the body to store up protein is limited. In such an animal, beyond the minimum required to make good the necessary katabolism in the cells protein can be utilized only to a small extent in the body as protein, and it is therefore rapidly katabolized, its nitrogen appearing in the urine as urea and other familiar end products. Nor is the situation essentially different in the growing or the milk-producing animal. While these animals are able to utilize considerable amounts of feed protein, yet the limit of this utilization is set by the normal rate of growth of the protein tissues or the capacity of the mammary glands to manufacture the casein and other proteins of the milk. Any surplus of protein over the amount which can be used for this purpose is katabolized precisely as is a surplus over the very small demand of the mature animal.

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[1] Henneberg and Pfeiffer. Journal für Landwirtschaft, vol. 38, p. 215.

As a single striking example there may be cited an experiment by Jordan,[1] in which the protein supply of cows, beginning with a liberal ration, was gradually diminished to about one-half and then gradually increased again to the original amount. The following table shows the average nitrogen balance of cow No. 12 of the second series of experiments, the daily results being grouped into periods as indicated.

Average daily nitrogen balance of cows—Jordan.

Date.	Number of days.	Nitrogen digested.	Nitrogen of milk.	Nitrogen of urine.	Gain by body.
		Grams.	*Grams.*	*Grams.*	*Grams.*
Jan. 30 to Feb. 6	7	186.6	81.7	87.0	+17.9
Feb. 6 to 16	10	185.2	81.4	87.5	+16.3
Feb. 16 to 26	10	161.6	77.5	81.9	+ 2.2
Feb. 26 to Mar. 8	10	130.8	74.0	56.5	+ .3
Mar. 8 to 18	10	117.2	66.6	43.7	+ 6.9
Mar. 18 to 28	10	143.6	69.6	61.8	+12.2
Mar. 28 to Apr. 7	10	171.4	71.6	89.2	+10.6
Apr. 7 to 14	7	185.7	71.9	104.4	+ 9.4

The amount of milk protein, like the total milk solids, diminished in quite a normal way with the advance in lactation, while the percentage of protein in the solids remained about the same. On the low protein rations of the middle periods there seems to have been some falling off in the amount of milk protein produced (and of the total milk solids as well) in comparison with what might have been expected on an unchanged ration, but the difference is small, except in one or two periods where the protein supply reached the lowest limit. Aside from this the principal effect of the variations in the amount of digestible protein supplied was to increase or diminish the amount of urinary nitrogen, which, as the table clearly shows, rose and fell with the supply of nitrogen in the feed.

PROTEIN AS A SOURCE OF ENERGY.

This increased katabolism of protein, however, is not to be regarded as a total loss of so much food material. The manner in which surplus protein is disposed of is rendered clear by a consideration of the chemistry of protein katabolism. Proteins are resorbed from the digestive tract in the form of comparatively simple cleavage products, chiefly amino-acids, and the body uses these nitrogenous cleavage products as building stones out of which to reconstruct body proteins broken down in the vital processes. As has just been shown, however, this necessary demand is relatively small, while the mature animal has lost the capacity which it had during growth of building up large amounts of new protein tissue. When the blood is, so to speak, flooded with these amino-acids in high protein feeding, some increase in the formation of body protein appears to result, as will be shown immediately, but this consumes a relatively small proportion of the nitrogenous matter and lasts for only a limited time. It is obviously an advantage to the organism, therefore, to be able to dispose of the surplus nitrogen. This it accomplishes by splitting off the NH_2 group and excreting it in the form

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[1] New York Agricultural Experiment Station, Bulletins 132 and 197.

of urea, etc., leaving a nonnitrogenous residue which contains the larger portion of the chemical energy of the protein which it represents and is in condition to be oxidized as fuel material. (Compare pp. 30–32.)

The increased nitrogen excretion on a high protein diet is simply the method by which the organism gets rid of useless nitrogen, while retaining the larger share of the energy of the protein for fuel purposes. In other words the organism when confronted with a protein supply in excess of its needs is able by what seems to be a comparatively simple process to transform it into nonnitrogenous fuel material with but slight loss, getting rid of the useless nitrogen as urea through the urine. The increased nitrogen excretion consequent on high protein feeding does not mean the total destruction of the corresponding amount of protein, but simply its transformation into compounds which can serve as sources of energy.

STORAGE OF PROTEIN.

In the mature animal a surplus of feed protein is largely katabolized, so that a continued increase of the protein tissue of the animal can not be brought about, as can that of the adipose tissue, simply by a surplus in the feed. The protein content of such an animal, however, is not to be regarded as absolutely fixed, so that the protein supply has no effect upon it. On the contrary, a considerable range of variation is possible.

When the protein supply is increased, nitrogen equilibrium is not established at once, but for a time more or less storage of nitrogenous material takes place. For instance, when a dog in Voit's experiments[1] was changed from a ration of 500 grams of meat daily for 42 days to one of 1,500 grams, the urinary nitrogen showed the following behavior on the last three days of old feeding and on the first seven of the new:

Storage of protein by dog—Voit.

	Date.	Meat fed.	Nitrogen of feed.	Nitrogen of urine.[2]	Gain of nitrogen.
	1863.	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Experiment No. 40	May 29	500	17.0	18.9	−1.9
	May 30	500	17.0	18.2	−1.
	May 31	500	17.0	17.7	− .7
Experiment No. 41	June 1	1,500	51.0	41.1	+9.9
	June 2	1,500	51.0	44.1	+6.9
	June 3	1,500	51.0	46.9	+4.1
	June 4	1,500	51.0	48.0	+3.0
	June 5	1,500	51.0	48.6	+2.4
	June 6	1,500	51.0	48.9	+2.1
	June 7	1,500	51.0	50.6	+ .4

Upon the lighter ration the animal was losing a small amount of protein daily. On the heavier ration there was a diminishing gain for six days, ap-

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[1] Zeitschrift für Biologie, vol. 3, p. 80.

[2] Computed from Voit's figures for urea.

proximate equilibrium being reached on the seventh day. The total gain in the seven days was 28.8 grams nitrogen, equivalent to 847 grams of fresh flesh, or about 12 per cent of the surplus fed, equivalent to from 3.5 to 4 per cent of the amount probably present in the body of the 35-kilogram dog.

In order to retain this protein which was stored up in the body, however, it was necessary to continue the heavier ration of 1,500 grams of meat. When, in previous periods of the same series, a ration of 1,500 grams of meat was followed by one of 1,000 grams and this by one of 500 grams, the protein previously stored up was rapidly katabolized again, as the following table shows:

Loss of protein by dog—Voit.

	Date.	Meat fed.	Nitrogen of feed.	Nitrogen of urine.[1]	Gain of nitrogen.
	1863.	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Experiment No. 38 (last 3 days)	Apr. 11	1,500	51.0	48.4	+2.6
	Apr. 12	1,500	51.0	50.9	+ .1
	Apr. 13	1,500	51.0	52.8	−1.8
Experiment No. 39	Apr. 14	1,000	34.0	38.6	−4.6
	Apr. 15	1,000	34.0	36.4	−2.4
	Apr. 16	1,000	34.0	36.4	−2.4
	Apr. 17	1,000	34.0	36.1	−2.1
	Apr. 18	1,000	34.0	34.3	− .3
	Apr. 19	1,000	34.0	35.2	−1.2
Experiment No. 40	Apr. 20	500	17.0	23.7	−6.7
	Apr. 21	500	17.0	20.4	−3.4
	Apr. 22	500	17.0	20.9	−3.9
	Apr. 23	500	17.0	18.8	−1.8
	Apr. 24	500	17.0	17.4	− .4
	Apr. 25	500	17.0	18.8	−1.8

The total loss of nitrogen from the body for the 12 days included in the table is 31 grams, or an amount about equal to that stored up in passing from the 500-gram to the 1,500-gram ration.

This comparatively small store of rapidly katabolizable protein in the body after liberal protein feeding Voit designated as circulatory protein, in distinction from the large mass of stable protein which he called organ protein. A variety of other names, corresponding to more or less definite theories as to the nature of the distinction between the two types of protein, have been proposed by later investigators, such as stable and labile, organized and unorganized, tissue and reserve, living and dead, protein. Still others, notably Gruber,[2] explain the temporary storage of nitrogenous matter in the body as due to a lag in the katabolism of protein, so that the splitting off of its nitrogen is not complete within the ordinary 24-hour period. The facts, however, that the nitrogen excretion follows in general the supply in the feed but that a temporary and limited storage of nitrogenous material in the body may result from liberal protein feeding, are undisputed.

FLUCTUATIONS IN BODY PROTEIN.

It is a familiar fact that a fasting animal may live and continue to perform the essential bodily functions for some time, while losing daily a not inconsiderable amount of protein. To cite a single striking example, Rubner observed in a fasting rabbit up to the time of death, on the nineteenth day, a loss of 45.2 per cent of the computed nitrogen of the body.[3] While this is an extreme case, neverthe-

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[1] Computed from urea.

[2] Zeitschrift für Biologie, vol. 42, p. 407.

[3] E. Voit. Zeitschrift für Biologie, Vol. 41, p. 139.

less it is evident that there must be a relatively large loss of body protein in those more moderate cases in which the deprivation of protein is not continued so long as to cause death. Furthermore, the losses occurring in these latter cases may be made good by subsequent feeding and the animal restored to its original state. Striking examples of the same fact are familiar in the human subject in the emaciation due to long illness and the restoration of the body during convalescence. Pugliese [1] has shown that a similar storage of protein takes place rather rapidly in the liver when a previously fasted animal receives feed again. In brief, it is evident that the body of the mature animal may fluctuate within somewhat wide limits as regards its protein content without necessarily causing any serious or permanent derangement of its functions.

We can hardly suppose such a fluctuation to consist to any large extent of an actual destruction and rebuilding of the cells of muscular or other tissue, but must regard it as effected chiefly by changes in the amount of cell contents—an alternate atrophy and hypertrophy of the cells under the influence of the changing protein supply. This same conception may be invoked, however, to explain small as well as large fluctuations in the body protein. According to Rubner,[2] the cells of the body seek to maintain an optimum protein content, and in proportion as this becomes reduced they show a capacity for storing up protein, when a more abundant supply is offered in the feed, which is analogous to that observed during growth. On the other hand, when the supply of feed protein is insufficient, protein previously stored may be katabolized.

In other words, as regards its stock of nitrogenous material the organism may exist and function at a higher or lower level according to the amount of protein supplied in the feed, while for each level of protein stock a certain supply in the feed is necessary—that is, the protein required for maintenance varies. With carnivora on a largely protein diet, such as was used in Voit's experiments, the adjustment of the body to the protein supply seems to take place rather promptly. In the case of herbivora, however, the adjustment appears to be more gradual, possibly owing to the relatively large supply of nonnitrogenous ingredients in their feed, and apparently some gain of protein may continue for a considerable time, although when expressed as a percentage of either the total feed protein or of the body protein the gain is relatively small.

RELATION TO ENERGY SUPPLY.

The prime demand of the organism is for energy for the performance of its vital functions, and if necessary it will draw upon its own tissues for this purpose. No clear conception of the laws

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[1] Jahresbericht über die Fortschritte der Tier-Chemie, vol. 34, p. 529.

[2] Das Problem der Lebensdauer, etc.

governing the protein metabolism can be reached without taking into consideration the energy relations.

Ordinarily, the nonnitrogenous nutrients of the feed constitute the principal source of this energy. The proteins, however, or at least the cleavage products of their digestion or transformation, readily undergo a process of deamidization by which their nitrogen is split off and excreted, leaving a nonnitrogenous residue which is available as a source of energy. It is evident, then, that the relative abundance or scarcity of the supply of nonnitrogenous nutrients to the cells of the body may profoundly modify the extent and character of the protein metabolism and consequently the magnitude of the protein requirement.

One instance of this effect is the so-called premortal rise of the protein katabolism of the fasting animal when the store of body fat is reduced below a certain level. (Compare pp. 12–13.) Here the relative deficiency of fuel material in the circulation causes an increased breaking down of the cell protein, presumably by hydrolytic cleavage and subsequent deamidization, its nitrogen being gotten rid of as urea, etc., and the nonnitrogenous residue serving as a source of energy in place of the lacking fat.

A precisely similar thing occurs when the nonnitrogenous nutrients in the feed are relatively deficient and is especially striking in their entire absence. It was pointed out on pages 75–78 that the protein katabolism during fasting is at least an approximate measure of the minimum protein requirement of the body, and that if this amount, or perhaps even less, be supplied in the feed, along with an abundance of nonnitrogenous material, the stock of protein in the body may be maintained. But if the experiment be made of supplying the minimum of protein without nonnitrogenous matter a very different result is obtained.

Thus in one such experiment by E. Voit and Korkunoff,[1] a fasting dog excreted about 4 grams of nitrogen per day, equivalent, of course, to a daily loss of about 24 grams of body protein, while in addition to this it must have been oxidizing considerable body fat. When, however, it was fed slightly more than 24 grams of protein[2] (4.1 grams nitrogen), with no other feed, its nitrogen excretion jumped to 5.56 grams per day, so that it was still losing daily 1.46 grams of nitrogen, equivalent to 8.76 grams of protein. Instead of the entire amount of protein in the feed being applied to make good the losses of protein tissue, over one-third of it was katabolized, its nitrogen appearing in the urine and its nonnitrogenous residue doubtless being used as fuel material. Protein rather more than equal to the 8.76 grams lost was then added to the ration, but again the protein katabolism increased and the body failed to maintain its stock of protein, and it was not until protein equal to about three times the fasting katabolism was fed that equilibrium was reached. The details of the experiments are shown in the following table,

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[1] Zeitschrift für Biologie, vol. 32, p. 67.

[2] In the form of lean meat from which the extractives had been removed by treatment with water.

the results furnishing also a striking illustration of the interesting relations between protein supply and protein katabolism which had been demonstrated more than 30 years earlier by the classic experiments of Bischoff and Voit.

Effect of protein supply on protein katabolism of dog—E. Voit and Korkunoff.

	Nitrogen in—		
	Food.	Feces and urine.	Gain (+) or loss (−).
	Grams.	*Grams.*	*Grams.*
Nothing	0	3.996	−3.996
Extracted meat (grams):			
100	4.10	5.558	−1.458
140	5.74	6.495	− .755
165	6.77	7.217	− .447
185	7.59	7.804	− .214
200	8.20	8.726	− .526
230	10.24	10.579	− .339
360	11.99	12.052	− .062
410	15.58	14.314	+1.266
360	13.68	13.622	+ .058

It is clear that in the protein-fed animal, as in the fasting animal, the demands of the organism for energy take precedence over the need for repair material, and that in default of nonnitrogenous material the protein of feed or of tissue is seized upon and katabolized for this purpose even at the expense of a loss of body protein, the body seeming to find it easier to do this than to draw upon the stores of fat in the adipose tissues.

What is so strikingly true in the total absence of nonnitrogenous nutrients holds good also in less degree in case of their relative deficiency. If a portion of the nonnitrogenous nutrients are withdrawn from a mixed ration, the protein katabolism usually increases, while, on the other hand, if nonnitrogenous nutrients be added to such a ration the tendency is to diminish the protein katabolism. This well-known influence of the supply of nonnitrogenous nutrients upon the protein katabolism, even in an abundant ration, is well illustrated by some of Kellner's respiration experiments on cattle,[1] in which starch was added to a basal ration. The following table shows the average daily gain of nitrogen by the animal on the basal ration and the increased gain following the addition of starch.

Effect of nonnitrogenous nutrients on gain of protein by cattle—Kellner.

Animal.	Gain of nitrogen.		
	On basal ration.	With addition of starch.	Difference.
	Grams.	*Grams.*	*Grams.*
Ox D	12.75	13.71	+ 0.95
Ox F	5.64	26.37	+20.73
Ox G	−.03	17.09	+17.12
Ox H	7.23	12.95	+ 5.72
Ox J	5.49	15.05	+ 9.56

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[1] Die Landwirtschaftlichen Versuchs-Stationen, Band 53.

It has been shown that this effect is produced not only by the true fats and by the soluble hexose carbohydrates, such as starch and the sugars, but likewise, in the case of herbivorous animals, by those ill-known ingredients of feeding stuffs, especially of the crude fiber and the nitrogen-free extract, which disappear in the passage of the food through the alimentary canal and which are commonly spoken of as being digested. This statement covers also the organic acids, whether resulting from the fermentation of the carbohydrates or contained in the feed.[1]

We are not, however, to conceive of a sharp distinction in this respect between an insufficiency and a sufficiency of nonnitrogenous nutrients, but rather of a tendency on the part of the latter to diminish the protein katabolism, a tendency more or less marked according to their abundance in the ration. We are not to understand that no nitrogenous material is katabolized for fuel purposes as long as sufficient nonnitrogenous nutrients are present to supply the demands for energy, nor that even the largest quantities of the latter can prevent the katabolism of protein supplied in excess of the possible constructive use by the body. We may believe that the protein cleavage products, either derived from the feed or from tissue katabolism, are always present in the blood and that more or less deamidization is continually going on, resulting in a use of protein material as fuel. On the other hand, nonnitrogenous substances, derived from the feed or the body fat, are also present and take their share in supplying energy. We may probably conceive of the quantitative character of the katabolism as being determined, in a very broad sense, by the law of mass action. An increase of nonnitrogenous materials in the blood or lymph tends to diminish the deamidization and subsequent oxidation of the cleavage products of protein and through this, secondarily, to diminish the breaking down of body protein or to stimulate and prolong the limited storage of protein possible in the mature animal.

As regards the maintenance requirement, it is evident, then, that the sufficiency of a given amount of protein depends not only upon the plane of protein nutrition of the body, but also upon the amount of nonnitrogenous nutrients supplied with the protein. With an abundant supply of the former an amount of protein equal to the fasting katabolism, or perhaps even less, appears to be a sufficient minimum for maintenance. As the supply of nonnitrogenous materials is reduced a larger supply of feed protein seems to be required to reach equilibrium because more and more of it is diverted for use as fuel, so that in the total absence of nonnitrogenous nutrients a large excess of protein must be fed before equilibrium between income and outgo is reached. In interpreting experiments or formulat-

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[1] Compare Armsby, Principles of Animal Nutrition, pp. 117–127.

ing a maintenance ration, therefore, it is not sufficient to consider simply the amount of protein, but account must be taken of the supply of nonnitrogenous materials.

VALUE OF NONPROTEIN.

The crude protein of the feed of farm animals includes not only true protein but a great variety of other nitrogenous substances, grouped for convenience under the designation "Nonprotein." In considering the results of experiments upon the protein requirements of these animals, therefore, it is necessary to determine whether the true protein should be the basis of comparison or whether the nonprotein has some value for maintaining the protein tissues of the body.

The writer has recently[1] considered in some detail the experimental evidence on this point, and the discussion need not be repeated here. It appears to have been demonstrated by recent experimental results, especially by those of Kellner, Morgen, and the Laboratory for Agricultural Research in Copenhagen, that the nonprotein of ordinary feeding stuffs is available for the maintenance of ruminants, probably indirectly through a conversion to protein by means of bacteria in the digestive tract. On the other hand, investigations have not thus far shown that such nonprotein has any material value for production purposes. The writer therefore reached the conclusion that for the present, pending further investigation, it is desirable to consider ordinarily only the digestible true protein in the computation of rations for productive purposes, ignoring the nonprotein. This implies, however, that a discussion of the results of experiments upon the protein requirement shall also be based upon the amounts of true protein supplied and not upon the crude protein. This will have two effects.

First, it will make the protein requirement appear smaller than it really is. Suppose, for example, that a series of trials in which the ratio of digestible nonprotein to digestible protein is 1:10 shows that nitrogen equilibrium is reached with a ration supplying 500 grams protein and 50 grams nonprotein. Regarding the true protein only, the maintenance requirement is 500 grams, while the real requirement of the animal is 550 grams.

In the second place, however, this error will be largely compensated for when the actual computation of rations is also based on the true protein. Thus in the case just supposed, if a maintenance ration be computed from any feed or mixture in which the ratio of nonprotein to protein is the same as in the experiments from which the maintenance requirement was deduced, viz, 1:10, it is obvious that the same final result will be reached whether the maintenance require-

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[1] Bureau of Animal Industry, Bulletin 139.

ment be considered to be 500 grams of true protein or 550 grams of crude protein. Only when the proportion of nonprotein to true protein varies widely from that existing in the rations used in determining the protein requirement will any significant error arise in computing rations.

In the results considered on succeeding pages, both the crude protein and true protein of the rations are stated when these are given in the reports of the experiments.

MINIMUM OF PROTEIN FOR FARM ANIMALS.

In considering the protein supply of different species of farm animals, it is important to distinguish between two points of view. On the one hand, it may be sought to determine the least amount of protein upon which the protein tissues of the animal can be maintained. This might be called the physiological minimum. It shows the proportion of protein in a productive ration which is devoted solely to maintenance. On the other hand, the endeavor may be to formulate the most advantageous amount of protein to supply when an animal is actually to be maintained for a time and this amount may very possibly be greater than the physiological minimum. The first point of view, however, is plainly the fundamental one and should receive our first consideration. Having determined the lower limit of protein supply, it will then be possible to consider intelligently the advantages, if any, of a surplus.

CATTLE.

For obvious reasons it is impracticable to ascertain the fasting katabolism of ruminants; their maintenance requirement as regards protein must, therefore, be determined by a process of trial.

The earliest, and for a long time the only, determinations of the maintenance requirements of cattle were those of Henneberg and Stohmann in 1858, the results of which as regards energy were cited on page 39. In 6 experiments the minimum amount of digestible crude protein (total nitrogen × 6.25) supplied per day was 0.35 pound per 1,000 pounds live weight and this quantity seemed to be more than sufficient for maintenance. On the average of the 6 experiments, in 2 of which there was some loss of body protein, 0.53 pound of digestible crude protein was consumed per 1,000 pounds live weight. Wolff's standard for maintenance, long current, viz, 0.7 pound digestible crude protein, was based on Henneberg and Stohmann's experiments with an allowance for the fact that their experiments were made at a relatively high temperature. Wolff's standard, however, was intended as a guide for actual maintenance feeding rather than as an expression of the minimum protein requirement.

In the light of later experience, the methods of these earlier experiments must be considered imperfect and their results are now chiefly of historical interest. The first experiments by modern methods were those of G. Kühn and

Kellner at the Moeckern Experiment Station,[1] which include determinations of the gain or loss of fat as well as of protein and hence afford a secure basis for judgment as to the sufficiency of the energy supply. Including subsequent slight corrections by Kellner,[2] the principal results as regards protein are summarized in the following table:

Gain or loss of protein by cattle—G. Kühn and Kellner.

No. of animal.	Live weight.	Protein per day and 1,000 pounds live weight.			
		Digestible in feed.		Gain by animal.	
		Crude protein.[3]	True protein.[4]	Protein.	Fat.
	Pounds.	*Pound.*	*Pound.*	*Grams.*	*Grams.*
II	1,394	0.65	0.58	−17.2	+ 75.8
III	1,393	.53	.35	−24.5	+ 63.0
IV	1,386	.53	.34	−25.9	+ 20.4
V	1,327	.75	.60	+21.8	+106.6
VI	1,420	.71	.57	+11.8	+119.3
XX	1,481	.80	.65	− 3.2	+ 71.7
A	1,365	.71	.56	+27.2	+103.0
B	1,348	.35	.28	−65.3	− 78.0

If the very small loss of protein by ox XX may be regarded as falling within the limits of experimental error, the eight experiments may be averaged as follows:

Animal.	Digestible in feed.		Gain by animal.	
	Crude protein.	True protein.	Protein.	Fat.
	Pound.	*Pound.*	*Grams.*	*Grams.*
Animals V, VI, XX, and A	0.74	0.60	14.4	+100.2
Animal II	.65	.58	−17.2	+ 75.8
Animals III, IV, and B	.47	.32	−38.6	+ 5.4

It appears that approximately 0.6 pound of digestible true protein or 0.74 pound of crude protein per 1,000 pounds live weight was at least sufficient to rather more than maintain nitrogen equilibrium when the total energy supply in the ration was sufficient to cause a small gain of fat, while half this amount of true protein or 0.47 pound of crude protein was manifestly insufficient. A reduction to 0.35 pound digestible true protein or 0.53 pound digestible crude protein in the cases of ox III and ox IV, even with a sufficient supply of non-nitrogenous material to cause some gain of fat, resulted in a loss of protein from the body, while in the case of ox B, with a slightly lower supply of true protein and a materially lower one of crude protein and a ration materially below the maintenance requirement, the loss of protein was still greater. The considerable loss of protein by ox II is not readily explicable.

Experiments upon the same subject were also made by the writer[5] in 1892–1898, chiefly upon rations of timothy or mixed hay, with the addition in Experiment VII of starch, but also, in Experiment VIII, upon a ration consisting

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[1] Die Landwirtschaftlichen Versuchs-Stationen, vol. 44, p. 257; vol. 47, p. 275.

[2] Die Ernährung der Landwirtschaftliche Nutztiere, 5th ed., p. 411.

[3] Corrected for estimated loss of nitrogen in drying of feces.

[4] As reported in the original account of these experiments.

[5] Pennsylvania Experiment Station, Bulletin 42, p. 165.

chiefly of grain together with a minimum of wheat straw. The results of these experiments are contained in the following table:

Nitrogen balance per 1,000 pounds live weight—Armsby.

Experiment.	Digestible in feed.		Nutritive ratio 1:	Gain or loss of nitrogen by body.
	Crude protein.	True protein.		
Experiment I:	*Pound.*	*Pound.*		*Grams.*
Steer 1	0.30	0.26	20.1	−2.7
Steer 2	.27	.23	20.4	− .4
Steer 3	.31	.27	18.6	−1.2
Experiment II:				
Steer 1	.45	.38	13.4	+1.9
Steer 2	.47	.40	13.6	+4.2
Steer 3	.49	.42	12.8	+5.2
Experiment VI:				
Steer 1	.62	.59	10.9	+4.7
Steer 2	.60	.55	10.9	+6.0
Steer 3	.67	.63	10.6	+2.8
Experiment VII:				
Steer 1	.49	.31	23.0	+5.7
Steer 2	.44	.26	25.3	+3.7
Steer 3	.51	.30	23.9	+4.4
Experiment VIII:				
Steer 1	.62	.52	10.4	+ .2
Steer 2	.57	.48	10.7	− .1
Steer 3	.66	.55	10.6	−2.0

In Experiments II, VI, VII, and VIII digestible crude protein ranging from 0.44 to 0.67 pound fully sufficed for maintenance, with a single exception. The range of true protein was somewhat wider, viz, 0.26 to 0.63 pound. The rations of Experiment VII were relatively richer in nonprotein than were those of the other experiments, and the adequacy of these very low protein rations suggests a utilization of the nonprotein, although the abundance of nonnitrogenous nutrients, as shown by the nutritive ratio, may also be a factor. The rations of Experiment I were obviously inadequate, even although the supply of nonnitrogenous matter was liberal.

Experiments upon a steer by Armsby and Fries[1] in which the respiratory products were determined gave results in general accord with those already cited. Computed per 1,000 pounds live weight, these results were as follows:

Nitrogen balance per 1,000 pounds live weight—Armbsy and Fries.

	Digestible.		Gain or loss by body.	
	Crude protein.	True protein.	Nitrogen.	Fat.
1902.	*Pound.*	*Pound.*	*Grams.*	*Grams.*
Period A	0.45	0.36	− 9.1	−286.5
Period B	.52	.42	− 1.3	− 89.2
Period C	.53	.44	− .4	+ .6
Period D	.68	.55	+12.3	+ 16.8
1903.				
Period I	.66	.46	−16.4	−192.9
Period II	.51	.38	−15.0	−350.8
Period III	.70	.53	− 2.3	−169.7
Period IV	.97	.84	+ 9.2	+196.4
1904.				
Period I	.44	.34	− 9.5	−312.7
Period II	.74	.55	− .8	− 75.2
Period III	.60	.46	− .5	−155.4

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[1] Bureau of Animal Industry, Bulletins 51, 74, and 101.

In periods C and D of 1902 and period IV of 1903, the only ones in which maintenance was reached, the crude protein ranged from 0.53 to 0.97 and the true protein from 0.44 to 0.84. In a later series of experiments[1] on two immature steers, from 0.92 to 1.13 pounds of crude protein, or 0.69 to 0.77 pound true protein per 1,000 pounds live weight sufficed for maintenance in three periods in which there was some gain of fat. The experiments furnished no evidence that so large an amount was necessary, since the next lowest amount was 0.44 pound crude protein or 0.37 pound true protein in a ration producing a slight gain of fat but a small loss of protein.

The investigations of the Laboratory for Agricultural Research in Copenhagen upon the protein requirements for milk production include also two experiments on dry cows[2] with rations furnishing relatively small amounts of digestible nitrogenous matter, chiefly in the form of true protein. The periods in which an approximate nitrogen balance was secured gave the following data:

Nitrogen balance of dry cows per day and head—Copenhagen experiments.

Cow and period.	Live weight.	Crude protein (N. × 6.25) digested.		Gain of nitrogen per head by animal.
		Per head.	Per 1,000 pounds live weight.	
Cow 117:		*Grams.*	*Pound.*	*Grams.*
Period 2	488	87.5	0.18	−3
Period 4	485	100.0	.21	+2
Cow 134:				
Period 1	466	143.8	.31	−5
Period 4	443	112.5	.25	+3

The experiments on milking cows also afford approximate data as to the maintenance requirement. If the protein of the milk is subtracted from the total digestible protein of the feed, the remainder is obviously the maximum amount which was available for maintenance. In Bulletin 139 of this bureau, pages 38–39, there are given the results of those experiments in which the smallest amounts of protein were consumed. Selecting from among these those in which there was an approximate nitrogen equilibrium, we obtain the results tabulated below:

Daily gain or loss of protein by cows—Copenhagen experiments.

Cow and period.	Live weight.	Crude protein digested.	Protein of milk.	Maximum crude protein available for maintenance.	Gain of protein by animal.
Sixtieth report:	*Kilos.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Cow No. 10, period 6	446	600.0	387.5	212.5	−12.5
Cow No. 53, period 4	454	543.8	350.0	193.8	−12.5
Cow No. 53, period 6	451	568.8	306.3	262.5	+18.8
Cow No. 68, period 4	461	575.0	393.8	181.2	−31.3
Cow No. 68, period 14	441	506.3	312.5	193.8	−12.5
Cow No. 58, period 4	485	531.3	325.0	206.3	− 6.3
Cow No. 58, period 6	485	581.3	293.8	287.5	+37.5
Sixty-third report:					
Cow No. 68, period 6	453	575.0	368.7	206.3	−25.0

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[1] Bureau of Animal Industry, Bulletin 128.

[2] Sixty-third Report, pp. 28 and 30.

In the two periods in which there was a gain of protein by the animal the crude protein available for maintenance, computed per 1,000 pounds live weight, was:

	Pound.
Cow No. 53, period 6	0.58
Cow No. 58, period 6	.59

In the four periods in which the loss of protein by the animal did not exceed 12.5 grams (2 grams nitrogen) the corresponding amounts were:

	Pound.
Cow No. 10, period 6	0.48
Cow No. 53, period 4	.43
Cow No. 68, period 14	.44
Cow No. 58, period 4	.43

These results are quite of the same order as those obtained by Kellner and by Armsby, while those on the two dry cows are much lower, with the exception of a single result of Armsby's. (Experiment I, steer 2.)

In drawing conclusions from the results recorded in the foregoing pages, it is important to remember that what it is sought to determine is the minimum protein requirement. As has been shown on previous pages, an excess of feed protein above this minimum is, in the case of the mature animal, substantially all katabolized, producing no material gain of protein. The fact of an equality of income and outgo of nitrogen upon a given ration of protein, therefore, while it shows that the quantity consumed is sufficient for maintenance does not show that a smaller amount would not suffice. What we have to consider is the evidence of the experiments regarding the least amount sufficient for maintenance. It is evident that this minimum amount is relatively small, but it is also evident that the recorded results do not suffice to fix with certainty the absolute minimum.

The lowest recorded amounts per 1,000 pounds live weight upon which nitrogen equilibrium was reached were 0.21 pound and 0.25 pound of crude protein in the Copenhagen experiments on dry cows, while almost as small a quantity, viz, 0.27 pound crude protein or 0.23 pound true protein in Armsby's Experiment I, steer 2, fell very little short of reaching nitrogen equilibrium. Aside from these somewhat exceptional results, the lowest figures obtained per 1,000 pounds live weight were 0.43 pound crude protein and 0.38 pound true protein. The maximum is found in Armsby and Fries' experiment of 1903–4, viz, 0.96 pound crude protein and 0.84 pound true protein, but it seems altogether probable that the animal in this period was consuming a surplus of protein. If we omit these few extreme results in either direction, the average and range of the results of the other experiments are as follows:

Average and range of protein requirements of cattle.

	Number of experiments.	Protein requirement.		
		Average.	Maximum.	Minimum.
		Pound.	*Pound.*	*Pound.*
Crude protein	19	0.55	0.75	0.43
True protein	12	.52	.63	.38

It seems safe, therefore, to estimate 0.6 pound of crude protein or 0.5 pound true protein per 1,000 pounds live weight as representing in a general way the minimum protein requirement of mature cattle with a probable range of 0.1 or 0.2 pound either way under varying conditions.

For actual maintenance feeding it is probable that a somewhat more liberal supply of protein than is indicated by these figures would be advisable. Rations so poor in protein, if containing an adequate amount of nonnitrogenous matter, would probably suffer a loss through failure of the animal fully to digest the nonnitrogenous matter. A somewhat narrower nutritive ratio could readily be reached in practice in ordinary feeding without additional expense and from the standpoint of digestibility would very likely be justified.

SHEEP.

While a considerable number of experiments with sheep are on record in which approximate maintenance as a whole was observed, at least so far as could be judged from the live weight, few of them afford satisfactory data as to the minimum protein requirement. For the immediate purpose of this discussion, only experiments in which the nitrogen balance was actually determined are available, mere maintenance of weight being too uncertain a criterion.

A distinct difference between cattle and sheep, which affects the protein requirement, lies in the greater demand for protein incident to the growth of wool in the latter animals as compared with that of hair in the former. The results of determinations by Armsby and Fries[1] on the same two steers in two consecutive winters showed an average production of epidermal tissue, including the growth of hair and the loss in brushings, equivalent to 0.19 gram nitrogen per day and 1,000 pounds live weight, which is equal to 0.0025 pound protein, an amount too small to materially affect our estimates of the maintenance requirement. In the case of sheep, determinations of the growth of wool by several investigators afford the following data regarding the average amount of protein required for this purpose. The results have been computed per 1,000 pounds live weight for the sake of ready comparison:

Protein contained in daily growth of wool per 1,000 pounds live weight.

		Pound.
Henneberg, Kern, and Wattenberg[2]	Mature sheep	0.132
Henneberg, Kern, and Wattenberg[3]	Lambs	.143
Weiske[4]	Growing sheep	.100
Henneberg and Pfeiffer[5]	Mature sheep	.149
Pfeiffer and Kalb[6]	Mature sheep	.150
Average		.135

Although, as the foregoing figures show, the protein requirements of sheep for the growth of wool are considerably greater than those of cattle for the

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[1] Bureau of Animal Industry, Bulletin 128.
[2] Journal für Landwirtschaft, vol. 26, p. 549.
[3] Ibid., vol. 28, p. 289.
[4] Landwirtschaftliche Jahrbücher, vol. 9, p. 205.
[5] Journal für Landwirtschaft, vol. 38, p. 215.
[6] Landwirtschaftliche Jahrbücher, vol. 21, p. 175.

growth of hair, the absolute difference, after all, does not add very greatly to the total maintenance requirement.

In Henneberg and Stohmann's Weende experiments[1] upon two sheep fed exclusively on meadow hay, there was digested on the average per 1,000 pounds live weight:

	Pounds.
Crude protein (total N × 6.25)	1.32[2]
Nitrogen-free extract	6.28
Crude fiber	3.93
Ether extract	.32

and the animal gained 0.17 pound of body protein, in addition to that stored in the wool, and a small amount of body fat.

In a series of 20 digestion and metabolism experiments by Schulze and Märcker,[3] decidedly smaller amounts of protein proved sufficient to maintain nitrogen equilibrium. In one case on a ration containing as little as 0.335 pound digestible crude protein per 1,000 pounds live weight, but having a very wide nutritive ratio (1:17.2) there was a slight gain of total protein, but one less than the amount required for the growth of wool. If we exclude this experiment and also 4 experiments in which it is evident that an excess of protein was fed, we have as the average of 6 experiments in which no loss of body protein was observed 0.653 pound digestible crude protein per 1,000 pounds live weight, while in two other experiments in which the minimum losses of 0.005 and 0.015 pound body protein were observed, the protein supply was, respectively, 0.655 and 0.690 pound. It is evident, then, that the protein supply of the sheep can be materially reduced below the amount fed in Henneberg and Stohmann's experiments without leading to a loss of body protein.

That such is the case seems to be clearly shown by the recent investigations of Katayama at the Moeckern Experiment Station,[4] in which increasing amounts of nearly pure protein ("aleuronat") were added to a basal ration very poor in protein, consisting of hay, oat straw, starch, and cane sugar. The protein in every case was substituted for a corresponding amount of starch, so that the total energy of the ration remained substantially unchanged. In the third period of the experiment both of the two sheep showed some loss of body protein, while in the fourth period, with more protein in the food, a gain was noted. In neither case was the growth of wool taken into consideration. By adding in the one case the loss of body protein to the digestible protein of the food and in the other period subtracting the gain, the author gets the following comparison:

Protein requirement of sheep per day and head—Katayama.

	Sheep I (weight, 34 kilograms).	Sheep II (weight, 38 kilograms).
	Grams.	*Grams.*
Period III:		
Nitrogen digested	1.978	2.412
Loss of body protein	.079	.216
	2.057	2.628
Period IV:		
Nitrogen digested	3.176	3.360
Gain of body nitrogen	1.107	.515
	2.069	2.845
Average for maintenance	2.063	2.737
Maintenance per 1,000 pounds live weight:		
Nitrogen	.061	.072
Protein	.379	.450

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[1] Neue Beiträge, etc.

[2] Estimated by Kellner to contain 1.04 pounds of true protein.

[3] Wolff: Die Ernährung der Landwirtschaftlichen Nutztiere, p. 300.

[4] Die Landwirtschaftlichen Versuch-Stationen, vol. 69, p. 321.

On the average of the two animals, 0.41 pound digestible crude protein per 1,000 pounds live weight was apparently sufficient to prevent a loss of nitrogen from the body. The crude protein in this case was practically all true protein, only minimum amounts of nonprotein being present in the ration. Since, however, the growth of wool must have gone on, with a corresponding storage of nitrogen, this apparent maintenance ration would really result in a loss of protein by the active tissues of the body.

If we add to Katayama's average 0.14 pound per 1,000 pounds live weight for the growth of wool, we get 0.55 pound as representing the minimum protein requirement for the maintenance of mature sheep, including the growth of wool. It is interesting to note that, according to these figures, the actual maintenance requirement for the body tissues is quite as low relatively as for cattle.

It is true that some earlier experiments seem to indicate a greater demand for protein than the foregoing figures show. Thus, in the experiments cited on page 80 to illustrate the influence of the protein supply upon its katabolism, a ration containing about 2.5 pounds digestible protein per 1,000 pounds live weight seemed to be about sufficient for maintenance, including the wool production, while a ration containing 2.27 pounds showed a loss of protein. Similarly, in earlier experiments by Henneberg, Fleischer, and Müller,[1] a ration containing 1.25 pounds digestible crude protein following one supplying 6.51 pounds resulted in a loss of protein by the animal. Notwithstanding these isolated results, however, it seems justifiable to accept the lower figure obtained by Katayama as representing approximately the minimum protein requirement of mature sheep.

SWINE.

The only data available as to the minimum protein requirement of swine are derived from the two experiments upon fasting animals by Meissl, Strohmer, and Lorenz (referred to on p. 51). The animals were Yorkshire swine, one 14 months old and weighing 140 kilograms, and the second, whose age is not given, weighing 120 kilograms. In the fasting state the nitrogen excretion of these animals was as follows:

	Live weight.	Nitrogen excretion.
Animal I:	*Kilos.*	*Grams.*
Average of first, second, and third days' fasting	140	9.80
Animal II:		
Average of third, fourth, and fifth days' fasting	120	6.77

The nitrogen excretion was equivalent, respectively, to 0.44 and 0.35 pound of protein per 1,000 pounds live weight, or about the amounts which appear to be required for cattle and sheep. No

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[1] Jahresbericht der Agriculturchemie, vols. 16–17, II, p. 145.

experiments are on record which demonstrate the sufficiency of this amount as a maintenance ration.

THE HORSE.

In the experiments by Grandeau and Le Clerc described on pages 62–63 the nitrogen balance of the horses was determined during 6 of the periods. The following table shows the amounts of protein and of nonprotein nitrogen digested in each period, the urinary nitrogen. and the small losses in epithelial tissue (epidermis, hoofs, hair, etc.):

Nitrogen balance of horses—Grandeau and Le Clerc.

	Horse No. 1.		Horse No. 2.		Horse No. 3.	
	January, 1884.	April, 1884.	November, 1883.	May, 1884.	December, 1883.	March, 1884.
Digested:	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Protein nitrogen	43.19	34.29	38.94	34.22	41.82	24.72
Nonprotein nitrogen	1.20	− 1.01	− 3.23	10.78	− 2.09	− 4.58
Total nitrogen	44.39	33.28	35.71	35.00	39.73	20.14
Nitrogen of epithelial tissue	1.46	1.46	1.46	1.46	1.46	1.46
Urinary nitrogen	35.17	38.75	30.70	41.92	37.62	32.70
Nitrogen gained	7.76	− 6.93	3.55	1.62	.65	−14.02

Omitting the results upon horse No. 3 in March, when the digestible protein was exceptionally low, the other five periods show an average daily gain of nitrogen of 1.33 grams, while the average crude protein digested (total N.×6.25) was 235 grams, equivalent to 0.59 pound per 1,000 pounds live weight.

THE OPTIMUM OF PROTEIN.

The data of the foregoing paragraphs seem to indicate a striking uniformity in the minimum protein requirement of the principal species of domestic animals when mature, 0.4 to 0.6 pound per 1,000 pounds live weight apparently sufficing to maintain nitrogen equilibrium under favorable conditions.

It should be clearly understood, however, that this figure represents a more or less accurately determined limit. It purports to be the amount below which the protein supply can not be reduced without eventual protein starvation. The animal body, however, may adjust itself to a wide range of protein supply above the minimum, using some of it to increase the stock of protein in the body and katabolizing the remainder as fuel material. An increase in the protein supply above the minimum results, after a relatively short time, in the maintenance of the body protein at a higher level. The practical question in actual maintenance is far less in regard to the least amount of protein which may be used than as to the most advantageous level of protein nutrition; that is, as to the optimum of protein.

This question has been warmly debated in connection with human nutrition.

Numerous recent investigations, notably those by Chittenden and his associates,[1] have shown that the protein of human dietaries can be reduced much below the amount previously regarded as necessary. In most cases there is no possibility of a direct comparison with the fasting katabolism of the same individual, but as previously stated (p. 77) a considerable number of instances are on record in which the nitrogen supply has been reduced to an amount materially lower than that usually found for the fasting protein katabolism of individuals of the same weight without leading to a loss of protein from the body. In all these experiments, the nonnitrogenous nutrients consisted, as is usually the case in human dietaries, to a considerable extent of carbohydrates.

Moreover, while some of the earlier experiments were for short periods and on comparatively few individuals, Chittenden's investigations covered long periods and were made on 26 different individuals, including 5 professional men under observation for 8 months, 13 soldiers observed for 6 months, and 8 trained athletes under observation for 5 months. His results clearly demonstrate the possibility of maintaining the body protein and fully preserving the health and vigor upon a low protein diet. In other words, a relatively low level of protein nutrition for several months is not inconsistent with health and efficiency.

In some of the earlier experiments in which very low protein diets were fed to dogs, the health of the animals suffered seriously and there has been a tendency to ascribe these ill effects to the continued use of very small amounts of protein. Later investigations by Chittenden, however, in which dogs were kept on a low protein diet for the greater part of a year, seem to have demonstrated that the ill effects observed in the earlier experiments were due to unhygienic conditions and not to the low protein diet. It may be remarked that in experiments upon cattle, rations very low in protein have been fed for a considerable time without any perceptible deleterious effects. No similar determinations upon other species of farm animals appear to have been made.

On the whole, then, it can not be said that a considerable surplus of protein over the minimum requirement for maintenance—that is, the maintenance of protein nutrition on a high plane—has been proved to be of any material advantage in the maintenance either of men or domestic animals during periods covering several months. Whether a continued low protein diet through years or generations would show a different result is at present largely a matter of speculation. It is to be remarked, however, that the particular point under discussion is the protein requirement of the mature organism. That a deficiency of protein in the diet of a growing animal may have disastrous results is clear. If, however, the habitual food supply of a race of men or a group of animals is low in protein, the young are likely to share this deficiency with the mature, and it seems not

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[1] Physiological Economy in Nutrition. Stokes Co., 1907.

impossible that this is an important factor in the alleged physical inferiority of certain races of men living on a low protein diet. This consideration warns us to exercise care in this respect in the management of the breeding herd.

In the actual maintenance feeding of farm animals, the matter of the digestibility of the ration must also be considered. It has been shown that a relative deficiency of protein in the ration tends to depress the apparent digestibility of both the protein and nonnitrogenous nutrients, especially in the case of ruminants. A maintenance ration for these animals containing the minimum amount of protein, together with the quantities of nonnitrogenous nutrients required to maintain the energy supply, would have a nutritive ratio, computed in the ordinary way, of approximately 1:12. On such a ration, there would, in all probability, be some loss of digestibility. An increase of its protein by 50 per cent would very probably effect a gain in digestibility which would more than offset the increased cost, if any. Indeed, unless feeds especially poor in protein are used, it may often be difficult, even if desirable, to reduce the protein content of a maintenance ration to the low level of absolute necessity.

RELATIVE VALUES OF PROTEINS.

In the discussions of the foregoing paragraphs, following the usual practice, the word protein has been used as if it designated a single chemical individual. In reality, of course, this is very far from being the case. The protein of the body or of the feed in this conventional sense includes a large number of distinct and in some respects, widely differing proteins. The studies of the chemical structure of the protein molecule made in recent years, beginning with the fundamental investigations of Emil Fischer, have shown marked differences in the proportions of the various "building stones" (amino-acids, etc.) contained in different proteins, while studies in immunity have led to the recognition of marked specific and individual biological differences in animal proteins, although these have not been definitely correlated with differences of chemical constitution. It is pertinent to inquire, therefore, whether we are justified in discussing the nutritive functions of feed protein as a group or whether we must consider each individual protein by itself. In other words, are there recognizable differences in nutritive value between individual proteins?

DIFFERENCES IN CONSTITUTION OF PROTEINS.

In discussions of this question, the chief emphasis has been laid upon the demonstrated differences in the proportions of the various cleavage products yielded by the different proteins when subjected to acid hydrolysis. The following table shows some of the more recent results obtained by Abderhalden and by Osborne:

Constituents of proteins—Abderhalden and Osborne.

Constituents.	Gliadin of wheat.[1]	Glutenin of wheat.[1]	Zein of maize.[1]	Phaseolin of white bean.[1]	Casein.[2]	Egg albumin.[2]	Serum albumin of horse blood.[2]	Serum globulin of horse blood.[2]	Ox muscle.[3]	Edestin from hemp.[4]
	P. ct.	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*
Glycocol	....	0.89	....	0.55	0.00	0.00	0.0	3.5	2.06	3.80
Alanin	2.00	4.65	....	1.80	.90	2.10	2.7	2.2	3.72	3.60
Amino-valerianic acid	.21	.24	....	1.04	1.00	....	....	(5)	.81	(5)
Leucin	5.61	5.95	....	9.56	10.50	6.10	20.0	18.7	11.65	20.90
Prolin	7.06	[6] 4.23	....	2.77	3.10	2.25	[1] 1.0	[1] 2.8	5.82	[6] 1.70
Phenylalanin	2.35	1.97	....	3.25	3.20	4.40	3.1	3.8	3.15	2.40
Aspartic acid	.58	.91	....	5.24	1.20	1.50	3.1	2.5	4.51	4.50
Glutamic acid	37.33	23.42	16.87	14.54	11.00	9.10	7.7	8.5	15.49	[7] 6.30
Serin	.13	.74	....	.38	.23	....	.6	....	(?)	.33
Tyrosin	1.20	4.25	....	2.17	4.50	1.10	2.1	2.5	2.20	2.10
Cystin	.45	.02	....	....	.06	.20	2.3	.7	....	.25
Lysin	.00	1.92	.00	3.59	5.80	....	....	....	7.59	1.00
Histidin	.61	1.76	.81	1.97	2.59	....	....	....	1.76	1.10
Arginin	3.16	4.72	1.82	4.72	4.84	....	....	....	7.47	11.70
Ammonia	5.11	4.01	3.61	2.06	1.95	1.63	....	....	1.07	....
Tryptophan	(5)	(5)	.00	(5)	1.50	(5)	(5)	(5)	(5)	(5)
Total	65.81	59.66	23.11	53.64	52.37	28.38	42.6	45.2	67.30	....

[1] Osborne. The proteins of the wheat kernel, pp. 110, 113, and 118.
[2] Abderhalden. Lehrbuch der physiologischen Chemie.
[3] Osborne. The American Journal of Physiology, vol. 24, p. 437.
[4] Abderhalden. Loc. cit.
[5] Present.
[6] A prolin.
[7] A later determination by Osborne (American Journal of Physiology, vol. 15, p. 333), confirmed by Abderhalden, gave 18.74 per cent.

While many of the figures of the foregoing table can not lay claim to a high degree of quantitative accuracy, it is, nevertheless, clear that the proportions of the various atomic groupings in the protein molecule vary within wide limits, while in some cases the most careful search has failed to show the presence of certain constituents. Thus, glycocol and lysin were not found in gliadin, nor lysin and tryptophan in zein, while ox muscle yielded a considerable percentage of lysin, a moderate amount of glycocol, and showed the presence of tryptophan.

ABSENCE OF CERTAIN CONSTITUENTS.

There is now a general agreement that in the process of digestion the proteins of the feed undergo extensive cleavage and are to a large extent broken down either into individual amino-acids or into comparatively simple peptid-like compounds. These substances are resorbed by the intestinal epithelium and the diverse proteins of the body are formed from them by synthetic processes, either in the intestinal wall or beyond. Such being the case, it has seemed clear that, for example, the proteins of ox muscle containing 2.06 per cent of glycocol and 7.59 per cent lysin could not be produced from gliadin, which is lacking in both these groups, nor from zein, which lacks lysin and tryptophan.

The classic example of the effects of such a deficiency is, of course, gelatin, which contains neither tyrosin, cystin, nor tryptophan. Bischoff and Voit[1]

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[1] Hermann's Handbuch der Physiologie, vol. 6, pp. 122 and 395.

long ago showed that gelatin in whatever amount fed is completely katabolized in the body, at least so far as its nitrogen is concerned, although it may somewhat diminish the waste of protein tissue. Subsequent investigations by Kirchmann[1] and by Krummacher[2] showed that when gelatin is fed alone an amount equivalent to the fasting nitrogen katabolism may reduce the loss of nitrogen from the body by something over 20 per cent, while, on the other hand, even very large quantities can effect a reduction of only about 35 per cent. Murlin[3] finds that in the mixed diet of men about two-thirds of the protein may be replaced by gelatin without disturbing existing nitrogen equilibrium. That the inferior value of gelatin is due to the absence of certain groupings in its molecule seems to have been shown by Kaufmann,[4] who found that gelatin with the addition of proper quantities of tyrosin, cystin, and tryptophan was able to maintain nitrogen equilibrium at least several days.

Investigations by Wilcock and Hopkins[5] upon zein, which, as already noted, lacks lysin and tryptophan, approach the subject from a slightly different angle. They found that a diet containing zein as its only protein material was unable to maintain growth in young mice. The addition of tryptophan approximately doubled the survival period and added markedly to the well-being of the animals, but was unable to maintain life indefinitely. On the zein diet the animals became torpid early in the experiment and almost comatose before death ensued, while with the addition of tryptophan no such symptoms were observed. The authors interpret this result as showing that tryptophan has some specific function in the body aside from the mere maintenance of nitrogen equilibrium. The results recently obtained by Osborne and Mendel,[6] however, show that great caution is necessary in the interpretation of such survival experiments, while they also indicate that growth is largely dependent on some other factor than the protein supply.

Experiments on rats by Henriques[7] gave a similar result as regards zein, with which it was found impossible to obtain nitrogen equilibrium in short experiments. On the other hand, however, an abundant supply of gliadin maintained nitrogen equilibrium for some days, notwithstanding the fact that it lacks both lysin and glycocol.

PROPORTIONS OF CONSTITUENTS.

Still further, even when all the constituents of the body protein are present in the feed protein, their proportions may be widely different. Thus, a mixture of equal parts of glutenin and gliadin would contain about 30 per cent of glutamic acid as compared with about half that amount in ox muscle, while the latter yields over 11.5 per cent of leucin as compared with less than 6 per cent from the former. In such a case it would seem that the tissues in which the synthesis takes place must make a selection from the material supplied by the digestive tract, reproportioning the various constituents, while the excess of certain ones would be attacked by the deamidizing enzyms of the body, their nitrogen being finally excreted as urea. Accordingly, it might be anticipated that the more nearly the feed protein resembled in its make-up the average of the body

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[1] Zeitschrift für Biologie, vol. 40, p. 54.

[2] Zeitschrift für Biologie, vol. 42, p. 242.

[3] American Journal of Physiology, vol. 19, p. 285; vol. 20, p. 234.

[4] Archiv für die Gesammte Physiologie des Menschen und der Thiere (Pflüger), vol. 109, p. 440.

[5] Journal of Physiology (London), vol. 35, p. 88.

[6] Carnegie Institute of Washington, Publication No. 156.

[7] Zeitschrift für Physiologische Chemie, vol. 60, p. 105.

proteins the more economically it could be utilized for the building up or repair of protein tissues, and that thus there might be very considerable differences in nutritive value between different proteins.

EXPERIMENTAL METHODS.

Considerations like the foregoing have been advanced by numerous authors, but as yet little satisfactory experimental work upon the relative values of the proteins has been reported. Indeed the problem is far from being an easy one. Aside from technical difficulties, it is, of course, a simple matter to substitute one protein for another in the ration; the difficulty lies in finding a satisfactory measure of the effects. The most obvious thing, of course, is a determination of the balance of income and outgo of nitrogen, which, when extended over reasonably long periods, affords an approximate measure of the relative gain or loss of protein. As has been clearly shown on preceding pages, however, the nitrogen balance, especially in a mature animal, is a more or less fluctuating thing, being materially affected by various factors besides the momentary protein supply. Especially important are the influence of the previous protein supply upon the general level of protein nutrition, the influence of the store of body fat carried by the animal, and the supply of available energy in the feed. Only after these influences have been eliminated as completely as possible can differences in the nitrogen balance be ascribed to differences in the nature of the proteins consumed. On this account, experiments in which additions of protein are made to a ration already containing a considerable supply and in which gains of nitrogen in different periods are made the basis of comparison are quite unsatisfactory, as Magnus-Levy[1] has pointed out. A more satisfactory basis of comparison is the amounts of the different proteins required to maintain nitrogen equilibrium under conditions otherwise comparable. Furthermore, the protein supply must not be too liberal. Protein supplied in excess of the minimum requirement is utilized largely as fuel material. Under such circumstances, it is easily conceivable that proteins differing widely in constitution may furnish enough of each of the essential cleavage products to meet the relatively small demand for the maintenance of tissue and that thus differences really existing may be masked by the excess of protein supplied.

These considerations clearly indicate that the most promising method of investigation is to compare the minimum amounts of the different proteins required, along with an abundance of nonnitrogenous nutrients, to maintain nitrogen equilibrium on as low a plane of protein nutrition as practicable in the same animal in like bodily states and under identical conditions, so far as it is possible to insure these. Any consistent differences appearing in a considerable number of trials may then, it would seem, be safely ascribed to differences in the nature of the proteins.

Thus far but three investigations, according to the general method just outlined, have been published, all of them appearing within the year 1909. For the present purpose it seems superfluous to review the older investigations, made by less satisfactory methods and in many cases from a different point of view.

MICHAUD'S INVESTIGATIONS.

Michaud[2] experimented on three dogs by substantially the method just outlined. Reasoning that any loss in transforming feed protein into body protein

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[1] Von Noorden's Handbuch der Pathologie des Stoffwechsels, vol. 1, p. 78.

[2] Zeitschrift für Physiologische Chemie, vol. 59, p. 405.

would be smaller the less the difference in the constitution of the two, he used as his standard protein supply either dog flesh or the ground flesh and internal organs (heart, liver, spleen, and testicles) of dogs. This material may be assumed to have supplied the various amino acids, etc., in approximately the proportions required to maintain the protein tissues of the experimental animals with a minimum of loss. With this were compared gliadin and edestin as representatives of the vegetable proteins differing quite widely from those of the body and casein as an animal protein more or less similar to the tissue proteins.

The series of experiments on the first dog affords a striking illustration of the difficulties in the way of successful investigation of this question. After fasting for 16 days and receiving only nonnitrogenous feed[1] (sugar and lard) for 28 days more, the daily nitrogen excretion (feces and urine) was reduced to 1.42 grams per day and appeared to have become approximately constant. Quantities of the various protein materials containing this amount of nitrogen were then added in successive periods to the basal nonnitrogenous ration and the effect upon the nitrogen balance determined, the periods covering from 6 to 9 days each. In three periods in which dog flesh was fed, the animal gained small amounts of nitrogen (0.08 to 0.17 gram per day); in other words, an amount of protein equal to the fasting katabolism sufficed to produce nitrogen equilibrium. Practically the same result was also attained in the period in which "Nutrose" (a preparation of casein) was fed. Three periods with gliadin, on the contrary, showed in every case a loss of nitrogen ranging from 0.33 to 0.52 gram per day; that is, the gliadin appeared decidedly less valuable than the dog flesh or casein for the maintenance of the body protein. Upon adding more gliadin to the ration it was found necessary to increase the daily amount to the equivalent of about 3.5 grams of nitrogen before nitrogen equilibrium was reached.

At the conclusion of this series, however, two 3-day periods on the nitrogen-free ration (preceding and following the period with the larger amount of gliadin) showed that the prolonged feeding on rations poor in protein had so lowered the plane of protein nutrition that the daily fasting katabolism was now equivalent to only 0.95 gram of nitrogen, or on the average of the last two days of each period to only 0.82 gram. In other words, the 1.42 grams of the earlier periods did not represent the absolute minimum on which life could be maintained. A second series of trials was therefore instituted in which dog tissue was compared with casein and edestin. In no case was nitrogen equilibrium quite reached, but the dog flesh still showed a decided advantage over the other forms of protein. The dog, however, had become very much reduced and died during the final period on dog flesh, the autopsy showing an exceedingly anemic condition. The attempt to base the comparisons of the different proteins upon the absolute minimum of the protein katabolism, in other words, involved such a reduction in the stock of body protein and consequently such an abnormal condition of the animal as to render the value of the results questionable. In succeeding experiments on two other dogs, therefore, the attempt to reach the absolute minimum of the protein katabolism was abandoned and the amounts of the several proteins added to the basal nonnitrogenous ration were either made equivalent to the fasting katabolism in the first period or reduced slightly below it according to the judgment of the experimenter. The results were in accord with those of the first series, the vegetable proteins, gliadin and edestin, proving notably inferior to the dog flesh or the casein.

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[1] No mention is made of any supply of ash ingredients other than those contained in the various forms of protein used, with the exception of a small amount of calcium carbonate (p. 423).

Upon two points, however, Michaud's results seem open to question.

First, the pure proteins which he employed, as well as the sugar and lard, can have contained but minimal amounts of ash, while, as already stated, no mention is made of the addition of any ash ingredients except calcium carbonate. In those periods, then, the animal was apparently in a state of partial or entire mineral hunger. The dog flesh (or in two periods horse flesh), on the other hand, contained its normal amount of ash, and it is not impossible that this was an important factor in determining its higher value, although it must be admitted that this explanation does not apply to the casein periods. Second, dog tissue or horse flesh is by no means pure protein, but in addition to ash constituents contains a great variety of organic compounds, which may have been quite as important as the protein. In other words, the periods on tissue are not comparable with those on pure proteins.

ZISTERER'S EXPERIMENTS.

Zisterer[1] has reported two series of similar experiments, also on a dog. They differed from Michaud's, however, in that the periods were shorter and that each feeding period was interpolated between two periods on a nonnitrogenous basal ration from the average results of which the fasting protein katabolism of the animal for that particular bodily condition was computed. Zisterer experimented with casein, wheat gluten, and lean meat extracted with water (muscle protein). He added to his rations the chlorids of sodium, potassium, and calcium, but no other ash ingredients. The ash content of the feeds was small. The energy supply in the feed was in every instance ample to supply the needs of the animal as computed according to E. Voit.[2] Taking the first period, on casein, as an example, the preliminary period on nitrogen-free feed covered five days and the one following the feeding period four days. On the average of the last two days of these periods, the fasting protein katabolism was equivalent to 1.975 grams nitrogen daily. During the intermediate 4-day period, casein containing 2.018 grams nitrogen per day was fed and the average daily nitrogen excretion for the last two days was found to be 2.333 grams. Two series of trials of this sort, made in inverse order, yielded the following results:

Protein metabolism of a dog—Zisterer.

	Fasting nitrogen katabolism.	Feed nitrogen.	Total nitrogen excretion.	Gain of nitrogen by animal.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Series I:				
Casein	1.975	2.018	2.333	−0.315
Muscle protein	2.125	2.021	2.316	− .294
Wheat gluten	1.951	2.017	2.113	− .096
Series II:				
Wheat gluten	1.800	2.111	2.276	− .165
Muscle protein	1.806	2.110	1.903	+ .207
Casein	1.708	2.108	2.050	+ .058
Average:				
Casein	1.842	2.063	2.192	− .129
Muscle protein	1.966	2.066	2.109	+ .043
Wheat gluten	1.876	2.064	2.195	+ .131

If we represent the total nitrogen excretion upon the muscle protein by 100, that observed with the other proteins was as follows:

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[1] Zeitschrift für Biologie, vol. 53, p. 157.

[2] Ibid., vol. 41, p. 113.

Relative nitrogen excretion on different proteins.

	Series I.	Series II.	Average.
Casein	101	108	104
Muscle protein	100	100	100
Wheat gluten	91	120	104

Compared in this way, the differences disclosed between the different proteins are small in themselves, and, especially in the case of the wheat gluten, are discordant in the two series. Apparently the differences are less than those which may be plausibly ascribed to variations in the conditions of the several experiments. The latter may be to some degree eliminated by comparing the total nitrogen excretion with the fasting nitrogen katabolism of the corresponding periods. If the latter be represented by 100, the relative nitrogen excretion on the several proteins was as follows:

	Series I.	Series II.	Average.
Casein	118.1	120.0	119.1
Muscle protein	109.0	105.4	107.2
Wheat gluten	108.3	126.5	117.4

This second method of comparison seems to indicate a distinct, although small, inferiority of the casein as compared with the muscle protein. The same is true of the average result with wheat gluten, but not of the results of the individual series. Entirely similar results are obtained if the calculation is made only upon the protein nitrogen of the feed and excreta instead of the total nitrogen. Zisterer's results are, of course, open to the same criticism made on Michaud's, viz, that the so-called muscle protein was not comparable with the pure proteins used in the other periods.

RESULTS ARE QUALITATIVE.

Both Michaud's and Zisterer's results are in a sense qualitative. They show that certain foreign proteins when substituted for tissue caused a relatively greater nitrogen excretion and were therefore less efficient in maintaining the nitrogen balance of the body. For gliadin and edestin, Michaud observed a notably greater difference than did Zisterer for wheat gluten. For casein their results are quite similar. In no case was the amount of foreign protein required to reach nitrogen equilibrium determined, with the exception of one short period upon gliadin in Michaud's experiments. In both cases, the differences appear relatively small. On the basis of average figures for the proportions of four of the principal amino-acids in the different proteins, Zisterer computes much greater possible differences. Representing the amount of muscle protein required to furnish a given amount of each one of the four amino-acids by 100, Zisterer calculates that the following amounts of casein and of wheat gluten would be required for the same purpose:

	Muscle protein.	Casein.	Wheat gluten.
To furnish equal amounts of:			
Alanin	100	444	267
Leucin	100	74	154
Glutamic acid	100	124	49
Tyrosin	100	47	102

As was noted above, the ash supply was but partially considered in Zisterer's experiments, no mention being made of the addition of ash ingredients with the exception of sodium, potassium, and calcium. It seems not impossible that the phosphorus compounds of the muscle protein may have had something to do with its apparently greater availability.

THOMAS'S EXPERIMENTS.

Thomas[1] has attempted to determine the relative values of the mixed proteins of different foods by a method differing somewhat from that employed in the two foregoing investigations. As has been shown in previous pages, on an abundant nonnitrogenous ration, especially of carbohydrates, the protein katabolism of the body may be reduced to a very low limit which represents more or less exactly the minimum amount of protein necessarily broken down in the vital activities. If a small amount of protein be added to such a nonnitrogenous ration, it will tend to be used to replace body protein, since the surplus of nonnitrogenous material tends to prevent its being katabolized to furnish energy. The extent, then, to which any given protein under these conditions diminishes the loss of protein from the body may be taken as the measure of its maintenance value. The principle of the method may be illustrated by the following supposititious case.

	On protein-free food.	On protein food.
Protein digested	0	4
Protein katabolized	6	7
Loss of protein from body	6	3

In this case, four parts of food protein obviously replace three parts of body protein and the percentage availability of the former is therefore 75. The principle of the method is similar to that of the determination of the percentage availability of energy (p. 27).

It is to be remarked concerning this method, first, that it assumes that the percentage availability of the food protein is the same for all amounts below the maintenance requirement; in other words, that it is a linear function. This is an unproved assumption, and in view of the readiness with which protein or its cleavage products in the body seem to be deamidized and utilized as fuel, the assumption seems of questionable validity.

Second, in applying the method it is necessary to know accurately the minimum amount of protein katabolized on a nitrogen-free diet, since any error in the determination of its quantity seriously affects the final result. The protein katabolism, however, under these conditions, is not a constant quantity, as has already been pointed out, but varies more or less, especially with the state of protein nutrition of the cells. Accordingly, it must be determined as accurately as possible for the subject at the time of the experiment, preferably immediately before and immediately after.

Third, the amount of protein fed must be less than that katabolized on the nitrogen-free diet. If an excess of protein be consumed, the additional amount will tend to be katabolized and used as fuel, thus rendering the comparison between the two periods illusory, since it is obvious that any such oxidation of protein would tend to make its availability appear too low. Thomas's experiments were made upon himself and included four series, two in May to

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[1] Archiv für (Anatomie und) Physiologie, 1909, p. 219.

July and two in September to November of the same year. He determined his protein katabolism upon a nonnitrogenous diet (chiefly carbohydrates) in three or four day periods in each series and also interpolated single nitrogen-free days during each series. The results of these periods were more or less variable, but the final values employed by him, although representing to some degree an arbitrary selection of days, seem, on the whole, to fairly represent the nitrogen katabolism; that is, they satisfy the second of the two conditions above pointed out.

With these values for the protein katabolism were compared the nitrogen balances of periods of from two to four days (or in a few cases only one day) in which single foods were consumed along with sufficient carbohydrates and fat to fully supply the demands of the body for energy. The technic of these periods, however, can hardly be regarded as entirely satisfactory. Out of 33 days, the results of which are contained in his final table, the protein digested was greater than the average protein katabolism on the nitrogen-free days in 21 cases, the difference sometimes being considerable and sometimes relatively insignificant. As already pointed out, this tended to make the availability appear too low, and it is noteworthy that the excess of food protein is especially large in the experiments upon wheat flour which show a strikingly low availability. On the other hand, however, it is also true that a very low availability was found for maize protein in experiments in which but a slight excess was fed. In these experiments, however, the apparent digestibility of the protein was remarkably low, ranging from 56 to 69 per cent, but a similar low digestibility (about 68 per cent) was found in the trials with rice. Furthermore, the periods were relatively short and in many instances the nitrogen intake varied considerably within the period, so that it may be questioned whether the nitrogen excretion reached a stable value. Moreover, to some extent there was a more or less arbitrary selection of days to be compared. For all these reasons Thomas's results must be accepted with more or less reserve.

His final results for the percentage availability of the protein of different materials are as follows, the results being calculated in three different ways, viz:

A. Fecal nitrogen all regarded as derived from the food, that is, the comparison is made upon the basis of the apparently digested protein.

B. Fecal nitrogen regarded as being all present in the form of metabolic products.

C. One gram of fecal nitrogen is regarded as derived from metabolic products and the remainder from undigested food.

Relative availability of proteins—Thomas.

	A.	B.	C.
Lean beef	104.94	103.75	....
	106.51	105.73	....
Milk	99.65	99.71	....
Fish	103.09	102.06	....
	85.73	89.37	....
	88.17	91.95	....
Rice	83.00	88.53	87.09
	86.26	90.73	89.55
Crabs	72.60	78.85	....
	73.38	79.45	....
Yeast	56.63	73.48	69.58
	53.40	70.35	71.45
Casein	66.69	70.14	67.12
Nutrose	63.45	69.02	....
Wheat flour	29.17	36.25	....
	36.70	43.04	....
	64.50	42.04	....
	41.35	51.10	48.97
	27.74	39.75	36.94

Relative availability of proteins—Thomas—Continued.

	A.	B.	C.
Potatoes	56.37		68.80
	64.50		72.67
	73.00		78.72
	80.33	83.18	
	77.04		76.22
	78.66		77.45
Cauliflower	80.68		87.78
	77.62		83.88
Spinach	64.50		63.83
Peas	49.58	59.89	55.15
	51.64	59.89	56.01
Cherries	66.42		78.57
Maize	24.55		40.47
	12.25		29.52
			3.54

In Zisterer's experiments, summarized on page 104, the feed nitrogen is so slightly in excess of the fasting nitrogen katabolism that it would seem that no large error would result from applying Thomas's method of computation. The results are as follows:

Percentage availability.

	Series I.	Series II.	Average.
Casein	82.26	83.77	83.02
Muscle protein	90.60	95.40	93.00
Wheat gluten	91.97	77.45	84.71

The results as thus computed are not widely different from those obtained by Thomas for casein and meat protein, but are slightly higher than his results for wheat protein. Michaud's results do not lend themselves to computation in this way.

Another recent investigation of a different character may be mentioned for the sake of completeness, viz, that on frogs by Busquet,[1] who compared lean veal and mutton with frog meat as regards the amount required to maintain the live weight or to produce a unit of gain of weight in previously fasting frogs. In this respect the veal and mutton were found distinctly inferior to the frog meat per unit of dry matter.

SIGNIFICANCE OF RESULTS.

In the comments upon the individual experiments, it has already been clearly indicated that they are open to criticism in many respects, such as the noncomparable nature of the protein supply, the lack of due consideration of the supply of mineral matter, etc. Moreover, nearly all the experiments were of relatively short duration.

Taking the results at their face value, however, they seem to indicate distinct differences in the nutritive values of proteins. The entire lack of certain groups, as in the case of gelatin and zein,

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[1] Journal de Physiologie et de Pathologie Générale, vol. 11, p. 399.

seems to render impossible a complete substitution for tissue protein, while differences in the proportions of the different amino acids apparently result in differences in the replacement values of the proteins, although these differences, especially in the experiments of Michaud and Zisterer, are hardly as great as might have been expected. What now can be said regarding the probable significance of these differences for the ordinary problems of nutrition?

In the first place, it is to be remarked that both man and animals consume a mixture of proteins. The meat eater gets, along with his gelatin, the various muscle proteins. The animal fed on maize alone receives not only zein but its associated proteins, amounting, according to Osborne,[1] to about 40 per cent of the total protein of the grain, whose chemical constitution has not yet been reported. In the ordinary mixed rations of domestic animals it would appear that there must be a considerable degree of compensation between the different proteins as regards the proportions of the different cleavage products supplied to the organism, although it is difficult to judge to what extent this is the case. In view, however, of the rather small differences observed with pure proteins, it may be questioned whether such differences as exist in mixed rations are of very much significance.

In the second place, the observed differences in proteins were obtained in experiments in which small amounts of protein were consumed and in which the animals were on a low level of protein nutrition. As was pointed out in the discussion of those experiments, the consumption of protein in excess of the maintenance requirement, such as usually occurs with domestic animals, tends to obscure the differences between the proteins, owing to the considerable extent to which protein serves for fuel purposes under those conditions.

Third, almost all writers upon this subject tacitly assume the inability of the body to change one amino-acid into another. It does not appear that there is adequate proof of this inability. Most of the amino acids concerned belong to the aliphatic series of compounds, characterized by a straight carbon chain, and as between these compounds, at least, mutual changes are not difficult to conceive. As a matter of fact one such change appears to have been demonstrated. It is well known that when benzoic acid is consumed it is paired in the body with glycocol, forming hippuric acid which is excreted. It seems to be well established that with large amounts of benzoic acid more combined glycocol may appear in the excreta than can be assumed to have been present as such in the amount of protein katabolized during the same time. In this case, apparently, the body is able to manufacture glycocol from some other substance, pre-

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[1] Journal of the American Chemical Society, vol. 19, p. 532.

sumably from the amino-acids containing a larger number of carbon atoms. Whether a change in the opposite direction, that is, a synthetic change, can take place can be at present only a matter of speculation, but such a change would be entirely analogous to the building up of the fatty-acid chains from carbohydrates, which is a common occurrence in the body. Moreover, Knoop,[1] and Embden and Schmitz[2] have found that certain amino acids may be formed synthetically from the corresponding fatty acids and ammonia, thus indicating a possible chemical mechanism by which a deficient supply of some one amino-acid might be to some extent overcome. While, therefore, we can hardly suppose that the proportions of the different cleavage products is a matter of entire indifference, we can easily imagine that there may be more or less transformation of one into another in case of need.

Finally, there is the possibility that in the absence of some one amino-acid from the feed, the corresponding acid resulting from the katabolism of protein tissue may to a greater or less extent escape the action of the deamidizing enzyms and be regenerated to protein. This would obviously be quite in accord with the conception of the protein metabolism as a complex of reversible enzym reactions which was outlined on page 87.

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[1] Zeitschrift für Physiologische Chemie, vol. 67, p. 489.

[2] Biochemische Zeitschrift, vol. 29, p. 423.

R. Hill