THE METABOLISM OF THE FASTING STEER

By

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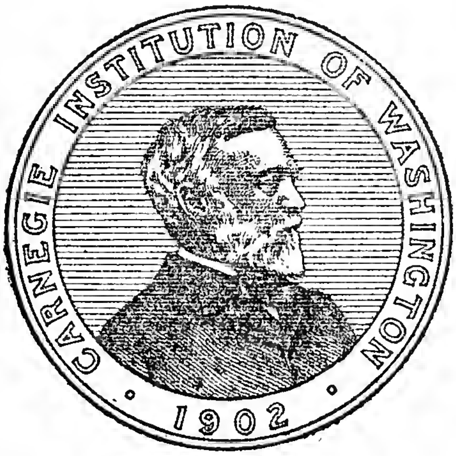
1902

Published by the Carnegie Institution of Washington
1927

CARNEGIE INSTITUTION OF WASHINGTON
Publication No. 377



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W. F. ROBERTS COMPANY
WASHINGTON, D. C.

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THE METABOLISM OF THE FASTING STEER

By F. G. Benedict and E. G. Ritzman

From the Nutrition Laboratory of the Carnegie Institution of Washington,
at Boston, Massachusetts, and the New Hampshire Agricultural
Experiment Station, Durham, New Hampshire

With eight text figures

INTRODUCTION

Much of the research in the field of human nutrition has been based upon experiments made during complete fasting. In this condition the minimum metabolism or the degree to which the body is drawn upon for maintenance of the life processes can be determined, and the capacity of any food or ration to protect the body from such drafts can then immediately be referred to the fasting metabolism. The seemingly inherent difficulties in subjecting a ruminant with large paunch to fasting has deterred most workers in animal nutrition from such tests, although as early as 1862 Hubert Grouven made his classic experiments with oxen, one of which fasted for 8 days.[a]

In the management of domestic livestock, farmers in the United States have been educated to believe that regular and liberal feeding forms the basis of good economic practice. This belief has not uncommonly led to the inference that animals deprived entirely of food, even for a relatively short time, would endure physical hardship, suffering, and injury. The error of such a conclusion is best illustrated by a consideration of the life habits of wild animals, such as the deer, which is also a ruminant. Deer pass through long periods of deprivation, when food is scant or sometimes entirely lacking, and on the whole survive in excellent shape, with remarkable vigor, unimpaired by such experiences. As pure *a priori* reasoning, it would seem logical to assume that the length of time during which an animal can comfortably go without food would be, at least in part, determined by its storage capacity, for until the food in the digestive tract is used up, complete fasting does not begin. The camel, due to his capacity for storage of water, has long been used for desert journeys. In a like, though limited, manner the ox has a storage capacity for forage and can exist without having his food replenished for several days before this storage is entirely depleted. The ox, however, is seldom forced by man to make use of this provision of nature, because it is usually more profitable not to do so.

The history of experimental fasting also shows that nature has provided animal life with a wide measure of protection against the contingency of food shortage. The almost incredible length of time that the dog has been able to withstand fasting, notably in the experiments of Howe and Hawk[b] whose dog fasted for over 100 days, and the long intervals known to elapse between the taking of food by cold-blooded animals, such as the large python in the New York Zoological Park[c] and the snake studied by Valenciennes,[d] lead to the inference that fasting *per se* is not ordinarily injurious, provided it is not carried to too great an extreme. All animal life does not, of course, possess the same degree of resistance to fasting, but it is safe to say that the resistance is far greater than is generally supposed. In the last

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[a] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmünde, Berlin, 1864.

[b] Howe and Hawk, Am. Journ. Physiol., 1912, 30, p. 174; Howe, Mattill, and Hawk, Journ. Biol. Chem., 1912, 11, p. 103.

[c] Unpublished experiments of Mr. Raymond L. Ditmars at the New York Zoological Park.

[d] Valenciennes, Compt. rend., 1841, 13, p. 126.

three or four decades much experience has been secured, both in the laboratory and also (as an incidental result of the recent World War) in large communities, regarding the effect upon humans of entire lack of food or of a greatly reduced food intake. This experience has indicated that, although in many instances serious disturbances may arise from such food shortage, unless the lack of food occurs at a very early stage of life, complete recuperation generally takes place fairly rapidly when sufficient food is again available. Indeed, we have seen that laboratory experience with animals shows innumerable instances of partial and of complete fasting for several months without ill results, and numerous observations on humans show that with some individuals complete controlled fasting may progress without injurious results for from one week to one month.[a]

The Nutrition Laboratory has for many years experimented with fasting. It has studied men who fasted for from 8 to 31 days, geese which were deprived of food for 30 days, and snakes which voluntarily refused food for a period of months. The general conclusion drawn from these experiments is that such fasting was not accompanied by pain, distress, or any untoward after-effects. This conclusion has been further confirmed by the extended experience of the Nutrition Laboratory in studying the effects of undernutrition upon a large group of young men. These men showed many striking, if not profound, physiological alterations due clearly to undernutrition, without a corresponding change in intellectual and physical powers.[b]

Having thus demonstrated the safety with which fasting and undernutrition may be practiced in humans, perhaps the most sensitive animal, the Nutrition Laboratory, in cooperation with the New Hampshire Agricultural Experiment Station, undertook a study of undernutrition in large steers, a report of which was recently issued.[c] This study likewise indicated clearly that undernutrition causes no distress or pain in cattle. An attempt to subject large ruminants to complete fasting seemed, therefore, in no sense open to serious objection.

THE SIGNIFICANCE OF THE FASTING METABOLISM OF CATTLE

As the result of feeding there occurs in the animal body a series of energy transformations which, from the economic point of view, represent at least four distinct phases of vital activity.

(1) The maintenance of life or body equilibrium.

(2) Productive use above the maintenance requirements, such as that for growth, milk production, and body deposits.

(3) Muscular activity, such as the productive muscular work of draft horses or oxen.

(4) The energy incident to the conversion of food or digestion.

The first bears directly on the extent to which food may serve to protect body-tissue from being drawn upon to maintain life and to replace body-tissue so used. The second relates to the extent to which food may be

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[a] Benedict, Carnegie Inst. Wash. Pub. No. 203, 1915.

[b] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919.

[c] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923.

converted into surplus body-tissue or into other usefully productive purposes above the needs of maintenance. Muscular work, when external, is a true production which may be of value, as in the draft animal, or may be waste, as in the restlessness or activity of the animal, even when in the stall. The internal muscular work of respiration, circulation, and digestive processes is an integral part of the necessary life processes of the animal, and hence a factor of maintenance. Productive muscular work must always be considered as a separate item, since it is performed at the expense of the production of body-tissue. It is equally clear that if the cost of food conversion, that is, the increase in heat-production following the ingestion of food, represents energy which does not serve to protect body-tissue or to form body-tissue, it must be regarded as an overhead cost physiologically.

The significance of studying the fasting metabolism under comfortable stall conditions, therefore, is that under these conditions the third and fourth uses of the total energy production are eliminated, and it is possible to determine the capacity of the energy in food to meet the first two needs.

Maintenance or fasting metabolism—The first function of food is to maintain life. Since the food, as eaten, requires considerable elaboration, cleavage, and resynthesis, an additional amount must be allowed to meet the energy expended in the conversion of the food; otherwise the ration will be deficient by that amount and body-tissue will be drawn upon to make up for the deficit. If no food at all is given, the entire amount of energy necessary to maintain life will be supplied by body-tissue. In this case the total energy production represents solely that quota of energy use which is necessary to maintain life, no overhead cost being included because no food is present. This fasting katabolism is the basic constant which must first be determined, before the energy uses for productive efforts and for overhead service can be reckoned separately. Furthermore, it is only on this fasting basis, when the metabolism indicates the daily heat requirements necessary to maintain life, that a comparison between different species or between animals differing in size or body-build is of any significance.

Productive use of food is represented by that measure of efficiency with which the animal is able to convert food, given in excess of its own need for maintaining body equilibrium, into some useful product such as growth, meat, milk, wool, or work. It is for this surplus production that domestic animals are kept, and it is on the basis of this surplus production that the efficiency of animals and of feeds is economically of variable significance. From a quantitative point of view the value of any given ration is in large part determined by the proportion of potential energy which it yields for conversion into body structure or milk.[a] A sufficient amount of protein is no less essential to carry on these functions successfully than is a sufficient amount of energy. Yet quantitatively the protein requirement never exceeds one-fourth of the energy requirement, even for growth or milk production, and for fattening purposes the quantitative relationship between energy and protein may even exceed a ratio of 10 to 1. The more recent knowledge regarding food-accessory factors is increasingly challenging attention also, but as far as now known their quantitative

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[a] Armsby, Journ. Agric. Sci., 1919, 9, p. 182.

importance is too small to be measurable. Hence it is not surprising that in general studies on nutrition the energy problems must continue to play the dominant rôle.

Muscular activity is a factor which makes an exceedingly marked demand on the use of energy. So far as tissue katabolism is concerned, there are several classes of muscular activity. Thus, the muscular activity which is involved in the mastication and general manipulation of food in the animal body is of a more or less involuntary character, and is to some extent proportional to food conversion, in behalf of which it is entirely exerted. It is an overhead expense, because it uses body-tissue which must be replaced by food, and as it can not be modified or controlled while animals are being fed, the determination of its quantitative demands on energy becomes complicated. Other types of muscular activity of a more voluntary nature are exhibited and measurable by the extent of visible manifestations, such as general restlessness and moving around. Such movements are in no sense contributory to food conversion. This type of muscular exertion may result in a greatly variable energy expenditure under ordinary conditions, not only when animals are grazing and thus obliged to move about according to the quality of pasturage, but also during the season of stall feeding, if they are allowed daily exercise. Unless the primary object in feeding animals for a usefully productive purpose is to enable them to perform physical exertion or work, as in the case of horses, mules, and work oxen, this type of muscular activity, if permitted, also becomes an overhead charge. In the study of nutrition problems, where muscular exertion is not the objective, this factor can easily be controlled within reasonable limits by placing the animals in stalls, so that voluntary muscular exertion is represented only by the tension due to standing and the effort of changing from the lying to the standing position.

The energy involved in food conversion, which is an overhead item, includes the energy expended in the actual physiological processes of mastication, digestion, and manipulation of food in the alimentary tract. It also includes a large daily energy production which occurs immediately when food is ingested or is present in the alimentary tract, inducing a stimulating effect on the body cells. Since, in this conversion of food, energy is consumed which would otherwise contribute to tissue equilibrium or towards other usefully productive service, this energy must be regarded as waste, just as undigested feed residues or the gases produced by fermentation are regarded as waste.

When food enters the alimentary tract there begins immediately a process which involves muscular motion, and, as is known, all muscular motion is accompanied by heat-production. Even the act of mastication results in a certain definite consumption of energy. The difficulties of measuring this latter exactly have led to wide divergence in the conception of the energy cost of mastication. With man a distinct rise in metabolism has been noticed as a result of chewing an inert, insoluble substance such as rubber or gum.[a] The subsequent processes of deglutition, peristalsis, expulsion of

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[a] Benedict and Carpenter, Carnegie Inst. Wash. Pub. No. 261, 1918, p. 139.

feces, and, in the case of ruminants, rumination, all involve muscular actions and, theoretically at least, heat-production.

The earliest studies with ruminants showed that there were great increases in energy production following the ingestion of food, increases which were at first attributed, naturally enough, to the slow passage of food through the alimentary tract and the vast amount of material to be worked over by peristaltic action. Indeed, Zuntz and his school believed that the increase was due in large part to the muscular activity involved in the propulsion of food from the mouth to the anus, although they freely recognized that there were subsidiary energy transformations necessitated by glandular and other processes. In the experiments with ruminants, the feed residues to be moved through the intestinal tract were very large, the indigestible matter amounting with rough fodders to 50 per cent of the intake. On the other hand, in experiments with humans and dogs, the diet contained a relatively small amount of indigestible material, and hence the increment due to the process of digestion could not logically be attributed to the muscular activity of moving a large food ballast. Furthermore, a careful study of the effect of individual nutrients, protein, fat, and carbohydrate, showed that protein caused a much greater rise in the heat-production of the dog or of man than either carbohydrate or fat. This difference was ascribed by Rubner to the "specific dynamic action" of the foodstuffs, and the two schools of Zuntz and Rubner have had long controversial discussions as to the causes for the increase in metabolism following the ingestion of food. It is not at all surprising that Zuntz, with his intimate knowledge of the physiology of the ruminant, should have attributed the large increase noted with these animals to muscular activity in connection with their enormous fecal masses and ballast. The amount of protein involved in the ration of many of these ruminants, and particularly in some of the special experiments of Zuntz, was so small as almost to rule out any material influence of protein *per se*. On the contrary, in Rubner's experiments on dogs, which were given large masses of nearly pure protein, the large increases noted in metabolism could not have been caused by the muscular action due to the process of digestion.

Since the promulgation of these earlier theories much experimental work has accumulated, chiefly with humans and laboratory animals, but at the present date information with regard to large ruminants is still sadly lacking. It is a fact, however, that the ingestion of food usually produces a marked increase in the heat-production of ruminants. Hence, in estimating the energy value of a given ration, one must immediately recognize that the increase in metabolism incidental to the digestion of the ration does not contribute to the production of either tissue or milk and must logically be charged as an expense in the preparation of the raw food material for deposition of tissue or for production of milk.

Although the processes of digestion, absorption, and peristalsis theoretically call for a consumption of energy, the demand for this purpose is probably very small. On the other hand, it seems clearly established that acid bodies are absorbed from the food which circulate in the blood and increase cell activity markedly, so that when food is supplied the cells are stimulated to a metabolic level considerably above that of the fasting animal.

This increase in cell activity resulting from the ingestion of food is likewise of no use to the body in preventing the oxidation of body material or in supplying energy for storage. Hence the energy represented by this increase in cell activity must also be deducted from the energy value of the food absorbed. It is not possible at the present date to explain clearly all the processes of digestion and the path taken by each individual component of the absorbed food. The investigations of Graham Lusk at the Cornell University Medical School are fundamental in this line. Thus far, unfortunately, they have been confined chiefly to the processes of digestion in the dog, with certain observations on man. A full understanding of the influence of such products upon cell metabolism in ruminants, however, can not be obtained by work upon carnivorous animals alone. The study of the after-effects of digestion in ruminants during the first few days without food, i. e., the beginning stage of fasting, is therefore of great importance, because it represents an entirely different type of digestive process.

DETERMINATION OF THE TRUE FASTING CONDITION

If food is withheld, the processes of metabolism to be measured will eventually become reduced to the process of katabolism. With animals having rapid digestion and absorption from the alimentary tract this stage is reached fairly soon, but with ruminants there may be a period of several days when the large ballast in the intestinal tract continues to add somewhat to the energy metabolism. Ruminants especially, therefore, should be studied, if possible, in the fasting condition in order to secure information on many problems. The determination of the true fasting condition, even with humans, is difficult. In the last analysis such a determination resolves itself into an attempt to find out for how many hours after the last meal the processes of digestion and absorption are active. The criteria for designating the exact time when true fasting begins are by no means sharply defined. In the case of adult humans cessation of digestion has commonly been considered to occur 12 hours after eating, provided that the last meal has not contained too large a proportion of protein. With infants, the period when absorption and resynthesis of absorbed material stop and the body begins to live solely upon previously formed body materials is determined only with difficulty.

One of the best indices of the true fasting stage with humans is the appearance of certain metabolic products, chiefly in the breath and urine, in the form of acid bodies. It is commonly believed that the appearance of acid bodies implies that free carbohydrate is no longer available for combustion, although blood-sugar is always present in normal amounts. In all probability the formation of these acid bodies is dependent not only upon the exhaustion of the supply of food carbohydrate, but upon the depletion or a heavy drain on the ever-existing store of glycogen. Because of this intermediary stage of depletion of carbohydrate storage, therefore, even these acid bodies are by no means sharp indices of the moment when fasting begins and the metabolism due to food particles ceases.

With infants, the onset of the true fasting condition, when food is not given, is rapid. Thus, after a relatively short time of fasting, acid bodies may appear. This fact has complicated greatly the determination of the true fasting metabolism of infants. The difficulty is by no means so great in the case of adult humans. A lengthy series of experiments has shown that the amount of glycogen drawn upon during the first day after the complete withdrawal of food may be as much as 100 or 200 grams, and that thereafter a continually decreasing amount is withdrawn until about the fifth day, when but about 20 grams enter into the metabolism.[a] Fasting metabolism, therefore, may not be described solely as a protein-fat katabolism, but more particularly as a metabolism in which body material furnishes the sole supply of energy. This material may or may not be organized body material, but at least it represents material which has passed out of the alimentary tract and has been absorbed, ready for further elaboration or combustion, as the case may be.

Because of the prolonged digestion of large food residues by ruminants, the attempt to establish a point as sharply defined as that just mentioned for humans has a greater element of uncertainty. The index of the formation of acid bodies may not be used in this case, for it is commonly believed that a large proportion of the fermentations taking place in the alimentary tract of the ruminant are accompanied by the formation of fatty acids which are subsequently absorbed and burned. However, knowledge of the influence upon metabolism of the absorption of fatty acids, and particularly knowledge regarding the appearance of fatty acids in the urine, is not without value in studying the metabolism of ruminants, as is shown in the consideration of the chemistry of the urine of steers (see p. 124).

Since a clear understanding of practically all the physiological processes of the animal organism, such as the digestion of food, the maintenance level of metabolism, and the productive level of metabolism, can be obtained only by reference to some level of metabolism of the animal which may be considered as reasonably fixed and well known, the determination of the exact time when the true fasting katabolism of large ruminants begins is therefore an important physiological study. In an earlier report such a reasonably fixed metabolism was defined as the "standard metabolism,"[b] and the beginning of the second 24 hours after the last meal was arbitrarily selected as the period of time when the greater part of the disturbing influence caused by the presence of food would have disappeared. With humans, 12 hours is considered a sufficient lapse of time, but it was obvious that with ruminants the slower passage of food through the intestinal tract would make it inevitably necessary to lengthen this time, although it was fully appreciated that the true fasting stage of metabolism could hardly have been reached in 24 hours.

THE PRACTICAL VALUE OF FASTING

The fact that a number of divergent feeding standards are now in use is, in itself, sufficient testimony that no standard has as yet been established which will meet conditions differing essentially from those under which it was determined. No doubt the main contributing causes for this failure to

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[a] Benedict, Carnegie Inst. Wash. Pub. No. 77, 1907, p. 463.
[b] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 197.

supply the producers of livestock with a standard of values of different feeds to meet the varying requirements in livestock production are found basically in the fact that the varying ways in which the animal organism expends energy have been either entirely ignored or have been computed on the basis of false assumptions, so that the true net use of food for conversion into body-tissue was not actually obtained. In other words, the physiological accounting has been faulty or incomplete in both cases. When the total available energy is accepted as the measure of productive use, the error lies in a disregard of the fact that different feeds have different conversion values. Thus, wrong net values, which alone are the measure of the effect of feed on animal tissue, were obtained. Consequently, since the overhead expenditure varies with different feeding-stuffs, all the factors which tend to obscure the net tissue-building value of a food must be determined separately. The factor of digestibility is easily measured, provided the experimental periods are long enough and the daily food-supply is constant enough to secure uniformity in the processes of digestion throughout the extensive, complicated digestive canal. The influence upon metabolism of the products of digestion is not so easily studied, and yet, as already seen, this must be most carefully taken into consideration. A large proportion of the energy of food absorbed is expended simply in a more active cell metabolism of the animal, and it is only that part of the food not expended in this increment which is of true use for the deposition of fat, flesh, or milk production, the main purposes of the beef-producing and dairy industries.

The true measure of this "overhead" in heat-production which must be charged against the processes of digestion and absorption has been sought in various ways. The experimental method of attack in studying the energy value of a food recognized that the fasting metabolism must be known, but assumed it could be computed. Thus, anticipating probable injury to the ruminant as the result of fasting, investigators have resorted to every other expedient to secure evidence with regard to the so-called true net available energy of foodstuffs. One method has been to estimate the fasting katabolism from a comparison of the metabolism on two different feed-levels, the observed difference in heat output being accredited to the difference in feed. The error of this method lies in the assumption that the metabolism proceeds as a straight-line function of the ration,[a] but there is no evidence on true fasting ruminants thus far published to support this assumption. In view of the enormous investment involved in beef and milk production, and in view of the fact that heretofore the economic valuation of foodstuffs has been determined by the method just outlined, a careful experimental investigation of the best method for determining the true value of food to the animal, i. e., by actual fasting, is imperative. Obviously the first step in such an experimental attack is to attempt to measure directly the *true* fasting katabolism of ruminants, and subsequently to use this fasting

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[a] Armsby (The principles of animal nutrition, New York, 1906, 2d ed., p. 430) cites the fact that his experiments on timothy hay are the only experiments of which he knew at that time which bear out this point. Nevertheless, he is inclined to think that this assumption is true, although he states that "the evidence of so few experiments must naturally be accepted with some reserve."

katabolism as the standard for studying the true effects of varying quantities of individual feeds.

The most logical method would seem to be to measure the fasting metabolism directly and then, by giving the animal various quantities of food, to study accurately the increase in metabolism due to each of these various amounts. Since the various avenues of energy-expenditure play relatively such an important rôle, an estimate of the value of any given food must be based on definite knowledge of the extent to which this food affects the standard or fasting metabolism. Does the ingestion of food increase the metabolism above this fasting base-line in direct proportion to the amount of food ingested? Is the fasting metabolism the same, irrespective of the state of nutrition previous to fasting? Is it affected by environmental temperature or by water consumption? These problems suggest that if the element of uncertainty introduced by attempts to establish the fasting metabolism through indirect methods could be avoided by actual measurement of the fasting katabolism, the whole complex problem of determining the specific value of various rations would be placed upon a sounder basis. The main object of the research reported in this monograph, therefore, was to throw positive light upon the pure fasting katabolism of large ruminants, and the first problem was a determination of the course of the metabolism in steers from the time when the last food is ingested until the fasting state is reached.

OTHER INVESTIGATIONS ON THE FASTING OF LARGE ANIMALS

Several fasting experiments have been carried out with large animals in the past, but, singularly enough, these are only rarely referred to in modern literature. This may be due to the fact that some of the investigators who have worked with large animals have published their results in remote and almost inaccessible publications. The fasting of a large animal (weighing 400 kg. or more) for several days affords the opportunity for such an important study, however, that the literature on the subject should be reviewed.

MAGENDIE, 1852

The earliest instance of the fasting of a large animal is that reported by Magendie.[a] A 9-year old mare, suffering from glanders, was deprived of all food, but was allowed 6 liters of water every 24 hours, which she drank each day until she died. Most of the observations had to deal with the blood, samples of which were taken frequently. Magendie does not comment on the general appearance of the animal during the first week of fasting. He states that on the eighth day the mare did not appear to have been affected appreciably by the fast, for she walked and ran about as usual. On the fifteenth day her physical condition was altered but slightly, and the decrease in flesh was hardly noticeable. Indeed, she was inclined to run about when allowed out of the stable. On the twentieth day the appearance of the animal had altered greatly. Her hair had changed color, grown longer, and bristled like that of a bear. She had the appearance of being blind, as the eyes had become glassy and seemed artificial. This change took place rapidly, but otherwise the animal was unusually vigorous. She was allowed to run around the stable yard, and upon hearing the crack of a whip began to run more rapidly. It was evident that she could stand a longer fast, although the heart-rate seemed feeble. The animal died, after 24 days of complete abstinence, except for 6 liters of water daily. Magendie considered that this experiment was only a preliminary trial, but that it seemed to open a new way to study. He suggested that it should be repeated, with frequent weighings of the animal, and especially with records of the body-temperature. The desirability of working on an animal without glanders is also pointed out. It is unfortunate that Magendie devoted so much attention to physical characteristics and the chemistry of the blood, for there must have been many other important observations that apparently escaped record.

COLIN, 1862 AND 1888

Although he did not study large ruminants, such as the steer, and made no measurements of the respiratory exchange, Colin[b] of Alfort (almost

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[a] Magendie, Leçons faites au Collège de France, 1851–52; collected and analyzed by Faugonneau-Dufresne, Paris, 1852, pp. 29 et seq.

[b] Colin, Bulletin Société impériale et centrale de Médecine vétérinaire, 1862, 7, 2d series, pp. 194 and 262; also Traité de Physiologie Comparée des Animaux, 3d ed., Paris, 1888, 2, pp. 682 et seq.

contemporaneously with Grouven; see pp. 15 to 20) reported the results of several fasting experiments with horses. A healthy, vigorous, moderately fat adult horse, weighing 405 kg., and with well-developed muscles, went without food completely for 30 days during the month of July, but drank water *ad libitum.* In 30 days he drank but 42 liters, or an average of 1.4 liters per day. Daily records were kept of the respiration-rate, the heart-rate, and the body-temperature. The total loss in body-weight was 80 kg. or 6.5 grams per kilogram of body-weight per 24 hours. The body-temperature remained essentially unchanged throughout the fast. Colin states that he will publish the details of his temperature measurements later, but unfortunately it has been impossible to find any such later publication.

On the thirtieth fasting day, although there was nothing to indicate that the horse would die, the animal was killed. The carcass gave the following data:

		kg.
Body		325.0
Blood	27.0	
Skin and hoofs	16.0	
Bone and cartilages	45.0	
Muscles and tendons	159.0	
Free fat	19.7	
Viscera	25.6	
Gastro-intestinal matter	26.2	
Loss	6.5	
Total		325.0

From this analysis Colin points out that the emaciation could have proceeded as much farther again. There was fat under the skin near the neck and shoulders, in the inguinal region, and on the buttocks. The fat in the abdominal cavity formed a layer 4 to 5 cm. thick and weighed, together with some fat in the breast, 14 kg. Fat was also found in the muscular interstices and large-sized globules of fat were found in the cells of the liver.

A small pony of 163 kg. (which had a case of glanders) fasted for 19 days in November. He lost 39 kg. during this time, or one-fourth of his initial weight instead of one-fifth, as in the case of the first horse. His daily loss in weight was double that of the first animal, i. e., 12.5 grams per kilogram of live weight.

Another horse, weighing 351 kg., which was slightly ill, lost in 18 days of fasting 89 kg. Colin believes he lost more than the pony, because he was very thin, and he lost twice as much per day as the horse which fasted for one month.

Another horse, weighing 504 kg., lost 65.5 kg. in 4 days of fasting, that is, 20.2 kg. during the first day, 13.8 kg. the second day, 16 kg. the third day, and 15.5 kg. the fourth day. He died on the fifth day, much more exhausted than the horse which lived for 30 days without food. But this horse had glanders, developed a fever, and instead of using up 6 grams per kilogram of body-weight daily he consumed 32.5 grams daily, or five times as much as the healthy horse. This is the largest loss Colin found with any of his horses and a loss which he thinks rarely takes place. This enormous "consumption" is explained by the febrile condition. Colin points out that, according to the analyses of Lassaigne,[a] a horse at rest burned 2,241 grams of carbon and as a result of exercise burned 4,887 grams or more than double, and he concludes that fever increases the expenditure of combustible body material just as muscular exercise increases the expenditure of combustible material obtained from foods. The chemical result is the same in both cases.

Still another horse, weighing 193 kg., which had undergone a slight surgical operation, lost 8.4 kg. per 24 hours during the first 2 days of fasting, or 43 grams per kilogram of body-weight per day instead of 6.5 grams, as in the case of the 30-day fast. But this loss for the first 2 days was much greater than that of the following days and should not be compared with the average value obtained during fasts of longer duration.

Colin remarks that large ruminants may lose in the same proportion and points out that a 1-year old heifer, weighing 146 kg., lost in the first days of fasting 4.3 kg. in 24 hours or 29 grams per kilogram of body-weight. It is unfortunate that the details are not given for the daily loss in weight, the water drunk, and the urine and feces passed, so that the insensible loss could be computed.

With the horse which fasted 30 days a study was made of the urine. At the beginning of the experiment the urine was thick, muddy with sediment, and alkaline. Hydrochloric acid brought about a quick effervescence and later the formation of crystals of hippuric acid. But at the end of a few days the urine had changed in appearance and character, becoming clear, transparent, and acid. In fact, the urine had the essential characteristics of the urine of a carnivorous animal.

Colin points out that it is a well-known fact that carnivora can withstand fasting better than herbivora. They are accustomed to frequent fasts and uncertainty in the securing of food and are therefore prepared naturally in some way for irregularity in eating, an irregularity much less frequently experienced by herbivora. The digestive tract of carnivora, which is not so large as that of herbivora, does not suffer from the lack of ballast. One meal supplies the carnivorous animal with food for a long time. When food from outside sources is lacking, food of a similar nature is available within the carnivorous animal itself. The origin of the food alone changes, but the kind of food remains the same. When herbivora are subjected to fasting, however, the character of alimentation is changed, for their own body-flesh must be consumed in place of vegetable material. The herbivorous animal therefore becomes carnivorous, for, not being able to derive any sugar or starch from food materials, he has to borrow from his own flesh to make up for this lack.

A remarkable fasting experiment with a rabbit is also reported by Colin. This rabbit fasted for 37 days without either food or water. His initial weight was 4,220 grams. On the thirty-seventh day he weighed 1,807 grams, or considerably less than one-half of his initial body-weight. This experiment is striking, since it is the common belief of investigators in animal physiology that rabbits withstand fasting poorly. Thus, experience with rabbits has shown that after a relatively few days of fasting there is an

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[a] Lassaigne, Journ. de Chimie médicale, 1846, 2, pp. 477 and 751; ibid., 1849, 5, pp. 13 and 253.

enormous increase in the breakdown of protein tissue, the so-called "premortal rise" in nitrogen excretion appears, and death follows rapidly thereafter.

Colin established the fact that young animals withstand fasting less successfully than do adult animals, in large part because their deposit of fat is much smaller. The influence of a fatty deposit was well shown in the case of a goose, which, with an initial weight of 4,800 grams, lived for 44 days without food, although receiving water *ad libitum.* At the end of this time it weighed 2,325 grams, or less than one-half of its initial body-weight. After death, 446 grams of free fat were found in the body.

Although the third edition of Colin's treatise was issued as far back as in 1888, his discussion of fasting animals may well be recommended to all workers in physiology. Unfortunately, data with regard to large ruminants are missing in his reports, but the fundamental principles underlying the influence of fasting (i. e., the effect of age and the effect of a fatty deposit) were strikingly brought out in his observations and his discussion of results.

GROUVEN, 1864

Among the earlier researches in nutrition the work of Hubert Grouven on the fasting metabolism of cattle demands especial attention, as it precedes any other similar investigation by nearly 60 years. Since his fundamental concepts of the study of nutrition problems are recognized as sound and essential to-day, it is unfortunate that his work has been unknown or disregarded during all these years by writers on animal nutrition.[a] Grouven's work may be summarized under the three separate phases in which he made notable contributions, namely, his general method of procedure and his physiological and chemical studies of the problems involved. His work is quoted here in some detail because of his sound grasp of the essentials involved in such studies and also to remove the possible impression that the idea of subjecting cattle to fasting as a requisite of nutrition studies is of recent origin.

Prior to Bischoff and Voit,[b] of whose work Grouven made extensive use, the nutritive value of a feed was based simply on the gains in live weight that the feed produced in the animal and no particular attention was given to the character of the gains or losses, the assumption being that they represented body-tissue. The fundamental incentive to Grouven's work lay in his recognition of the fact that great changes occur in the gross live weight of an animal which have no bearing whatsoever on changes in body-tissue. Convinced that the nutritive value of food must therefore be expressed directly in terms of the gain or loss of muscle-tissue and fat, he studied the problem from this point of view, thus making a radical departure from previous methods of investigation.

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[a] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmünde, Berlin, 1864. Unfortunately, these experiments were reported in a publication rarely found in American libraries, and it is because of the inaccessibility of these data that we review his report here in somewhat greater detail than seems necessary in the case of those writers whose works are more generally available and known.

[b] Bischoff, Der Harnstoff als Maass des Stoffwechsels, Giessen, 1853; Bischoff and Voit, Die Gesetze der Ernährung des Fleischfressers durch neue Untersuchungen, Leipzig and Heidelberg, 1860.

Method of procedure—Grouven's method of attack involved a complete physical and chemical study of the contents of the digestive tract of the ruminant. This study served as a physiological basis, by means of which the relative effects of different feeds on body-tissue and on the feed residues in the alimentary tract could be determined separately, since both are manifested in terms of live weight. He planned to study the nutritive value of numerous individual materials in a pure form, such as sugar, starch, and dextrine. He realized, however, that these could not be fed to a ruminant without roughage or bulk, as such a feed alone would upset digestion. Accordingly he decided that the nutritive effects of a standard roughage, such as rye straw, must first be determined. Then straw, plus a definite amount of the special purified food material, was to be fed. To establish the influence of a basal ration of roughage, such as rye straw, he reasoned that the fundamental starting-point or base-line would be represented by the fasting state only, i. e., when no food is present to stimulate the metabolism. Thus, he made his greatest contributions in the execution of an experimental plan based on this conception, i. e., the necessity of establishing a base-line as a preliminary to subsequent investigations. Grouven began his first experiment in 1862, with 2 oxen and 2 cows, feeding each of them with a basal ration of 3.5 kg. of rye straw for a period of 2 weeks. He assumed that by the end of that time any undigested residues from previous feed would have been eliminated and that the fill or residues in the

TABLE 1.—*Live weight, water intake, and excreta of fasting oxen, and contents of digestive tract before and after fasting (Grouven)*

Measurement	(*a*) Average for 2 cows	Brown ox		Black ox		(*f*) Average for 2 oxen (*b*+*d*)+2
		(*b*) After fasting 5 days	(*c*) Loss (*a*−*b*)	(*d*) After fasting 8 days	(*e*) Loss (*a*−*d*)	
Live weight:	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*
Start of fast	398	420	....	522	....	471
End of fast	....	381	....	480	....	431
Loss	....	38.7	....	42	....	40.4
Water intake	....	14.3	....	35.4	....	24.9
Urine	....	29.2	....	26.7	....	27.9
Feces	....	15.9	....	17.2	....	16.6
Contents digestive tract (fill):						
Water	52.76	38.61	14.15	66.06	....	....
Dry matter—						
C	4.217	0.976	3.241	1.097	3.120	....
H	0.549	0.128	0.421	0.139	0.410	....
O	3.527	0.818	2.709	0.921	2.606	....
N	0.131	0.036	0.095	0.053	0.078	....
Ash	0.969	0.439	0.530	0.584	0.385	....
Total dry matter	9.393	2.397	6.996	2.794	6.599	....
Total fill	62.15	41.01	21.14	68.85	....	54.93
Fat	0.287	0.045	0.242	0.048	0.239	....
Cellulose	3.007	0.717	2.290	0.694	2.313	....
Water (per cent)	85	94	....	96	....	....

alimentary tract would have a constancy characteristic of the daily ration, i. e., that it would be the same in all four animals. The water intake was likewise controlled, but only during the last four days, when each animal was allowed 7.5 kg. daily. The oxen then fasted, one for 5 days and the other for 8 days. The cows, on the other hand, were slaughtered and a careful analysis was made of the quantity and character of the contents of the alimentary tract. The oxen were slaughtered at the end of their respective fasts and similar analyses were made.

Physiological considerations—By this experiment Grouven contributed the first physiological data showing the effect which quantitative changes in feed produce on the character and the amount of fill. Assuming that the contents of the digestive tract of the two oxen would be the same at the beginning of the fast as that of the two cows which were slaughtered at that time (all four animals having received identical amounts of rye straw and water), he calculated the amount of material disappearing from the digestive tract during the fast by deducting the amount found at the end of fasting from the amount present at the start, and from this he determined the amount assimilated from the straw during the fast, as shown in Table 1. Grouven's data bring out some significant physiological facts regarding fill, or the feed residues in the alimentary tract. Practically nothing definite was on record at that time regarding the total amount of fill in cattle, and information regarding the effect of changes in feed on fill was equally lacking. The values for total fill, which he records for his cows (not fasting), correspond closely to the figures obtained by Moulton about 50 years later. His analysis of the quantitative changes in fill that occur in different parts of the digestive tract throws new light on the course of absorption, as indicated by the data in Table 2. The fact that the quantitative change during fasting is least in the stomach and paunch and greatest in the large intestine suggests that the excess moisture in the fill was largely absorbed before the fill was voided. This finding offers an explanation for the occurrence of exceedingly dry feces in our own fasting and submaintenance experiments. One of the outstanding features shown by Grouven's data is the great increase in the moisture content of fill in the fasting animal, which tends to offset the loss in dry matter. A further point of significance is the fact that although identical amounts of rye straw and water were consumed by the

TABLE 2.—*Influence of fasting upon the contents of the digestive tract of oxen (Grouven)*

Contents of—	Average for 2 cows (not fasting)		Ox (5-day fast)		Ox (8-day fast)		Average for 2 oxen	
	Kg.	P. ct. of live weight	Kg.	P. ct. of live weight	Kg.	P. ct. of live weight	Kg.	P. ct. of live weight
Stomach and paunch....	48.3	12.1	34.9	9.1	59.4	12.4	47.1	10.8
Small intestine.........	5.5	1.4	3.3	0.9	5.0	1.0	4.1	0.9
Large intestine.........	8.5	2.1	2.9	0.8	4.5	0.9	3.7	0.8

two oxen previous to fasting, the difference in their fill at the end of fasting amounted to about 70 per cent, due in a large measure to the difference in water consumed during the fast. In other words, the assumed constancy of the conditions affecting live weight, on which he based many of his subsequent calculations, was not materialized.

Fasting metabolism—From the decrease in the fecal excretion during the fasts and the analysis of the fill at slaughter, Grouven concluded that complete fasting began on the fifth day. The results of his experiments with 5 oxen are given in Table 3. Since the loss of muscle-tissue was computed from the urinary nitrogen in the usual manner, the nitrogen requirement of about 50 to 60 grams daily (equal to from 1.5 to 1.8 kg. of body-flesh) noted on the fifth day without food, apparently represented the true basal nitrogen requirement during fasting in his experiments. Grouven reasoned that during fasting the flesh and fat metabolism of the animal would be depressed to a minimum level, which would not be difficult to recognize because of its constancy. Moreover, he believed that the heat-production calculated from the loss of flesh and fat under this condition of minimum use would also be the same in all those experimental conditions in which the animals would be given rations somewhat below maintenance, and that they would therefore have to supplement the ration with fat and flesh from their own bodies. His determination of the fat metabolism during fasting appears somewhat vitiated, because of his computation of the probable loss of body-fat from changes in live weight by using Voit's equations, the weakness of which he recognized. His attempt, however, to correct the defect due to dependence on live weight by a careful analysis of the different factors that collectively must represent the changes in gross live weight, that is, the insensible perspiration, represents a real contribution to the study of nutrition problems.

TABLE 3.—*Data for insensible loss, respiratory exchange, and heat-production, as derived from metabolism equations (Grouven)*

Ox	Days fasting	Average body-weight[1]	Total loss in—		Per 24 hours			Respiratory quotient	Heat produced per 24 hours	
			Flesh	Fatty tissue	Insensible loss	Carbon dioxide production	Oxygen consumption		Total	Net[2]
		kg.	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*		*cal.*	*cal.*
Black.......	8	501	9.74	11.84	4.19	4.66	4.50	0.75	[3]14,850	[3]13,325
Brown......	5	403	5.21	4.99	1.56	3.79	3.52	.78	11,620	13,540
Ox I (1861)..	3	431	2.32	3.33	7.16	4.70	4.31	.79	14,225	12,995
Ox I (1862)..	4	521	3.16	5.48	3.17	4.79	4.62	.75	15,245	13,230
Ox III (1861)	3	523	4.43	3.38	4.45	4.99	4.57	.79	15,065	13,550

[1] Average of initial and end weights.

[2] Reduced to uniform conditions of 450 kg. body-weight, 15° C., and 3.5 kg. vaporized water.

[3] Our computation of Grouven's data gives values slightly different from these.

Insensible perspiration—Grouven's critical determination of the water balance by means of Voit's so-called "control calculations," based, however, on his own analysis of the fill of slaughtered animals, represents up to the present the only attempt on record (except our own data) to measure in ruminants the daily insensible losses (in large part water-vapor) through the lungs and skin. This attempt recognized the great rôle which water plays in the variations in live weight, and also points out the possibilities of the insensible perspiration serving directly as a measure of metabolism. In other words, having determined the water intake, the water voided in feces and urine, and the resident water in the digestive tract before and after fasting, Grouven determined the amount and the constancy of the water lost in vaporized form as perspiration. He pointed out that this so-called "insensible perspiration," or invisible daily deficit, is always consistent on a given feed-level and represents an invisible loss which presumably can find no other means of escape except through the lungs and skin. The source of this particular loss, as Grouven points out, is derived from the loss of muscle or fatty tissue and of water preexisting in the body. The direct form in which it is lost is largely water-vapor and gaseous products. He assumes, therefore, that the insensible perspiration represents purely the by-products of tissue katabolism and not carbon dioxide from the process of tissue replacement. Hence he considers differences in the amount of water perspired by different animals as the result rather than as the cause of differences in heat-production.

Chemical problems—Based on his exhaustive chemical studies of the fill, Grouven concluded that none of the carbohydrates are absorbed unchanged into the blood and directly contribute to the nutritive processes, but that they are entirely assimilated in the form of fatty acids and glycerides, which are formed only in the presence of alkaline solutions, i. e., primarily in the small intestine. This revolutionary theory regarding the path of the absorption of carbohydrates is, as a matter of fact, wholly unrecognized even to-day, save for a reference to it by Zuntz.[a] There is considerable evidence in more recent investigations supporting this theory. Although the isodynamic law of replacement had not been established at that time, Grouven found that the consumption of protein was smaller when rye straw was fed than during complete fasting, thus forecasting the possibility that fat and carbohydrates (for amount absorbed see Table 1) may protect body protein.

Conclusion—In view of the comprehensive basis upon which Grouven's work was planned and the extreme care with which it was carried out, and in view, furthermore, of the fact that his whole work was finally computed by means of Voit's metabolism equations based on live weight, probably his most noteworthy permanent contribution is made in his own summary statement, which follows a discussion of the uselessness of accepting live-weight records at the beginning and end of a test as a measure of the effect of any given food.

"The indisputable fact remains that it would never become possible to explain the results of experimental feeding on the basis of scientific facts

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[a] Zuntz, Internat. Agrartechnische Rundschau, 1914, 5, Heft 4.

or to apply the results of experimental feeding successfully to general practice without a knowledge of the effect of food on the metabolic exchanges which take place in muscle-tissue, fat, water, and mineral salts, a knowledge which can be obtained only by means of a respiration apparatus and metabolic balances."

The potency of this statement, which amounts practically to an acknowledgment of weakness of his own metabolism measurements, lies in the extraordinary thoroughness in detail with which his experiment was planned and carried out.

IGNATIEF, 1883

Ignatief, in 1883, studied the influence of fasting upon the body-weights of steers.[a] Thus, 85 steers, which were being transported from Karlovka to Moscow and thence to St. Petersburg, were divided into three groups. One group received food and water, the second water only, and the third neither food nor water. The animals were weighed just prior to transportation, were weighed again at Moscow, when they had been in the cattle cars for 6 days, and again at St. Petersburg, 3 days later. A comparison of the average loss in body-weight of the different groups, on the percentage basis, is given in Table 4. The actual body-weights are not recorded by Ignatief.

TABLE 4.—*Percentage loss in body-weight of steers during 9 days of partial or complete fasting (Ignatief)*

Food condition	Percentage loss in body-weight		
	First 6 days	Last 3 days	Total for 9 days
Food and water	3.11	5.6	8.71
Water only	3.67	6.2	9.87
No food or water	9.16	3.8	12.96

Ignatief points out that the fasting steers which received water lost less weight than those that received neither water nor food, and probably would have lived longer if the fasting had been continued until death. He states, however, that water is favorable during fasting only for steers and, to a certain extent, rabbits, but for other animals water during fasting is sometimes harmful. Evidently no records other than body-weights were obtained by Ignatief.

MEISSL, 1886, AND TANGL, 1912

Although our report deals primarily with the effect of fasting on ruminants, brief mention is justifiable here of the fasting studies with large swine carried out by Meissl and Tangl. In 1886, Meissl,[b] working at the agricultural experiment station at Vienna, published the results of one 3-day

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[a] Reported by Pashutin, General and Experimental Pathology (Pathological Physiology), St. Petersburg, 1902, 2, Part 1, p. 156. English translation of Pashutin's book is on file in the Nutrition Laboratory.

[b] Meissl, Zeitschr. f. Biol., 1886, 22, p. 104.

fast with a male hog weighing 144 kg. and one 5-day fast with a male hog weighing 122 kg. A respiration chamber employing the Pettenkofer principle was used, and measurements of the carbon-dioxide production were made. Later, in 1912, Tangl[a] subjected 4 male swine, two 7 months old (40 to 50 kg.) and two 1¼ years old (110 to 120 kg.), to fasts lasting from 5 to 9 days. During this time the carbon-dioxide production, the production of water-vapor, and the nitrogen, carbon, and energy in urine were determined at definite intervals. The respiration chamber for average-sized animals at the experiment station for animal physiology at Budapest was employed, an apparatus which combines the principles of the Pettenkofer-Voit, Atwater-Benedict, and Tigerstedt respiration chambers. The influence of environmental temperature upon the carbon-dioxide production was one of the factors studied.

CAPSTICK AND WOOD, 1922

The heat-production of a male hog was measured in the calorimeter described by Capstick[b] during six fasts, each of from 4 to 6 days in duration, at environmental temperatures ranging from 10° to 20° C.[c] The observations extended over a period of 114 days. The hog was 10 months old at the beginning and weighed 100 kg.; at the end he weighed 155 kg. During the feeding-periods (usually about 2 weeks long) between the fasts the food was of the same general character, but was increased gradually so as to be roughly proportional to the two-thirds power of the animal's weight. The hog received 7.5 liters of water daily while fasting. Readings of the various instruments were taken at hourly or at half-hourly intervals, when the galvanometer curve showed that the hog was asleep. At the conclusion of the experiment the curve and the readings were carefully studied, to find the times at which the metabolism was at a steady minimum. Considering the variation in the age and weight of the animal during the period of observation and the range of temperature in the different experiments, the authors conclude that the rate of change of the resting metabolism at any moment depends only on the time elapsed since the last meal and is independent of the age and weight of the hog and the temperature of his surroundings. The data show that the basal metabolism of the hog was not reached until the fourth day of fasting. The results of these same experiments were used by Capstick and Wood later[d] as the basis for a study of the effect of change in temperature on basal metabolism. The critical temperature of the hog was found to be 21° C. At this temperature the basal metabolism was minimum and amounted to 2,160 calories in 24 hours, when he was 420 days old and weighed 136 kg. This corresponds to 904 calories per square meter of body-surface per 24 hours. As the environmental temperature decreased below the critical temperature, the basal metabolism increased at the rate of about 4 per cent per degree Centigrade, which corresponds to an increase of approximately 40 per cent for a temperature difference of 10° C. (commonly found between summer and winter conditions).

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[a] Tangl, Biochem. Zeitschr., 1912, **44**, pp. 235 and 252.

[b] Capstick, Journ. Agric. Sci., 1921, 11, p. 408.

[c] Capstick and Wood, Proc. Roy. Soc. London, Ser. B, 1922, **94**, p. 35.

[d] Capstick and Wood, Journ. Agric. Sci., 1922, **12**, p. 257.

If the same law holds in the case of a steer, whose basal metabolism at 18° C., or summer temperature, is 6,000 calories, his basal metabolism at 8° C. in an open yard in winter would be 9,000 calories. It is suggested that the increase of 3,000 calories is met by the utilization of the thermic energy of the coarse fodder included in the ration.

DEIGHTON, 1923

Employing the calorimeter for large animals (devised by A. V. and A. M. Hill and improved by J. W. Capstick) at the Cambridge School of Agriculture, England, Deighton[a] studied the metabolism of a pig while fasting, at various ages from 75 days to about 1½ years. The fasting was in some instances prolonged to 104, 109, and even 116 hours. The pig weighed 12.7 kg. at the start of the experimental season, when 75 days old, and 137.4 kg. at the end of the season, when 483 days old, and fasted on 12 different occasions. The author in this really excellent research concludes that in the pig, as in human beings, the metabolism per unit of surface area is greater in mid-youth than at any other time of life, a fact which is directly ascribable to growth. The metabolism following the ingestion of food reached its maximum after 5 hours and then declined.

ARMSBY AND BRAMAN, 1923–24

An abstract of results on fasting experiments with 2 cows, carried out under the direction of Professor H. P. Armsby, of the Institute of Animal Nutrition at State College, Pennsylvania, was reported by us in our first monograph.[b] The details of these experiments had not been published by Professor Armsby at that time, but permission was given us by him to cite his findings. In 1924, following Professor Armsby's death, Braman[c] reported the results of fasting experiments with 5 cows, including revised figures for

TABLE 5.—*Carbon-dixoide, heat, and methane production of fasting cows (Braman)*

Cow	Time without feed	Produced per 24 hours		
		Carbon dioxide	Heat	Methane
		gm.	*cal.*	*gm.*
886 IV	24 to 48 hours	2,223	6,743	27.4
886 IV	48 to 72 hours	1,987	6,328	11.8
885 IV	24 to 48 hours	2,247	6,750	33.5
885 IV	48 to 72 hours	2,148	6,557	17.4
885 III	5 days[1]	2,034	6,577	5.8
887 III	9 days[1]	1,885	6,061	2.8
874 III	9 days[1]	2,091	6,302	4.1

[1] The values given for cow 885 III represent an average for the fourth and fifth days of fasting; those for cows 887 III and 874 III represent averages for the eighth and ninth fasting days.

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[a] Deighton, Proc. Royal Soc., London, 1923, Series B, 95, p. 340; apparatus described by A. V. and A. M. Hill, Journ. Physiol., 1914, 48, p. xiii, and later by Capstick, Journ. Agric. Sci., 1921, 11, p. 408.

[b] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, Table 66, p. 256.

[c] Braman, Journ. Biol. Chem., 1924, 60, p. 79.

the two earlier experiments which Professor Armsby had privileged us to cite. Braman's data are summarized in Table 5.

These experiments were carried out to furnish additional data on the ratio of carbon-dioxide to heat-production in cattle, concerning which an earlier report[a] had been published in 1920, dealing, however, only with cattle on feed. As a result of these fasting experiments and other experiments with very low feed intake new equations were derived, which, Braman states, confirm the previous conclusion:

> "The amounts of carbon dioxide and heat produced are approximately linear functions of the feed. . . . As the feed increases the amount of heat produced does not increase as rapidly as the amount of carbon dioxide produced. In other words, the ratio of carbon dioxide to heat has its maximum in fasting, and decreases quite regularly, but slowly, with increase in feed. This gradual change in the relation of the amount of carbon dioxide and heat produced is caused by variation in the proportion of the kinds of nutriment, from the ration and from the body, which are metabolized."[b]

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[a] Armsby, Fries, and Braman, Proc. Nat. Acad. Sci., 1920, **6**, p. 263.

[b] Braman, Journ. Biol. Chem., 1924, **60**, p. 88.

CHANGES IN APPARATUS AND TECHNIQUE

Our research was carried out with the equipment as described in our earlier monograph.[a] Certain significant modifications and additions made since that time need special consideration and recording here.

CHANGES IN THE LABORATORY BUILDING

Arrangement of laboratory rooms—The general floor plan of the laboratory for animal nutrition is shown in Fig. 1. The main floor is divided into four rooms. The room on the right contains the respiration chamber *A*, the Bullock scales *M*, and the water tub *N*. Adjoining this, but separated by a double wall, is a small room containing the aliquoting table *B* and the balance *D*, for weighing the soda-lime and Williams bottles. The long, narrow room to the left of this, on the front of the building, contains the gas-analysis apparatus on the bench *E*, the switch board *T*, and shelves and storage facilities *U*. The large room back of this contains the two metabolism stalls, showing feed boxes *K, K*, the traps for feces *L, L*, and the holes *H, H*, through the floor for insertion of urine tubes.

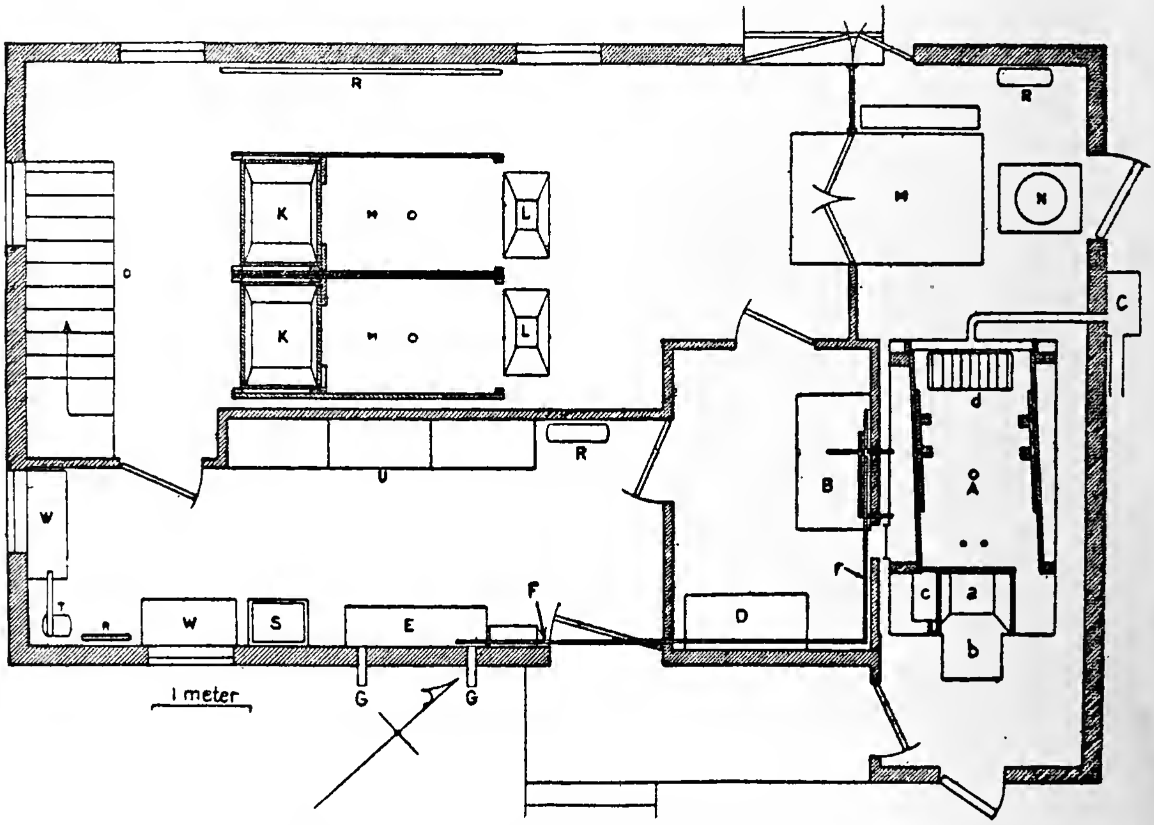

Fig. 1.—Arrangement of laboratory rooms

Respiration chamber *A*, with feed-box *a*, feed-chute *b*, water-trough *c*, and feces grid *d*; *B*, aliquoting table; *C*, blower delivering outdoor air into chamber; *D*, table holding balance for weighing absorber bottles; *E*, bench containing several gas-analysis apparatus; *F*, pipe delivering samples of air from aliquoting table to gas-analysis apparatus; *G*, *G*, tubes through which samples of outdoor air are drawn for control tests of the gas-analysis apparatus; *H*, *H*, metabolism stalls with urine tubes in center; *K*, *K*, feed-boxes; *L*, *L*, feces traps; *M*, scales for weighing steers; *N*, water-tub; *O*, stairway to basement; *R*, *R*, *R*, *R*, radiators; *S*, sink; *T*, switchboard; *U*, shelves and closets for supplies; *W*, *W*, tables.

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923.

Control of environmental temperature—The importance of studying the influence of environmental temperature made necessary facilities for a reasonably exact control of the temperature in the metabolism stalls and in the respiration chamber. These facilities are supplied by an adequate steam radiation, whereby a temperature of not less than 30° C. can be maintained even during the coldest weather, and by five windows and three doors, the opening of which will bring about a reduction of the temperature to a point closely approximating the outdoor temperature. When the chamber was installed in this building, space was provided on all four sides for free circulation of air. The room containing the respiration chamber can be shut off from the room containing the metabolism stalls by double doors, and it is thus possible to maintain entirely unlike temperature conditions in the two rooms, if desired. In lieu of a much preferred automatic control, this type of temperature control served reasonably well. Owing to the wide range of climatic conditions in America, this temperature control is a very important factor in the study of the effect of variations in environmental temperature upon the metabolism of beef animals. Unfortunately, with the forms of respiration calorimeter thus far devised, the environmental temperature can be altered within only a few degrees, and it would seem as if this problem must be attacked by means of respiration chambers in which the temperature of the air can be greatly altered, or else a new type of calorimeter must be devised to meet this important condition.

Motor-generator set—Although an alternating current can for the most part be used as well as a direct current, if a number of magnets are employed a direct current is necessary, particularly in the regulation of the electrical by-pass. The entire equipment at Durham has therefore been arranged with motors requiring a direct current. The regular commercial 110-volt alternating current drives a motor connected to a direct-current generator (110-volt) by a single shaft. The motor-generator set is installed in the basement of the laboratory. Although it is believed that a direct current is most advantageous for the working of the apparatus as a whole, it is always possible to arrange for the actuation of the several magnets by storage batteries and to use an alternating current for the motors.

PROVISION FOR COLLECTION OF INDIVIDUAL URINATIONS

The method of collecting the urine by attaching an ordinary urine funnel to the animal and passing the outlet tube through the floor of the metabolism stall to receptacles below has been described in an earlier report.[a] The receptacles commonly used are 5-gallon carboys, each of which rests permanently on the balance of a scale. Since in many experiments, particularly in fasting, it is essential to know the time when the urine is voided, as well as the quantity, a simple electrical contact was installed by which a bell is rung when a fresh flow of urine passes and raises the balance-arm of the scale. This bell continues to ring until the carboy is again exactly counterpoised and the contact on the balance-arm broken. By this means it is possible to record not only the exact moment of each urination, but likewise the exact weight of the urine voided. The scales, which are also used for

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 28 and 32.

weighing feces, are the so-called "silk scales," weighing to 125 kg. The beam has 10-gram graduations for a beam range of 2 kg.

ADDITIONS TO RESPIRATION CHAMBER

The respiration chamber, as originally designed and used, had no provisions for feeding and watering or for the collection of urine and feces, since it was planned primarily for short 2-hour experiments. Even during the long fasts of 5 to 14 days the respiration experiments were only of 2 hours' duration. It was considered desirable, however, to have a complete record of all excreta voided during these fasts, and the first change in the chamber was therefore made to provide for the collection of excreta while the animal was inside the chamber. On the basis of the gratifying results obtained during the continuous 3-day experiments in April and May 1924, it was decided to lengthen the experiments from 2 to 24 hours or to several continuous 24-hour periods. Furthermore, it was found highly desirable to be able to run experiments in which the animal could be fed and watered as usual for a day or more, and then be subjected to fasting, in order to observe on succeeding days the influence of food on the one hand and the withholding of food on the other hand, on the expenditure of energy. Because of this change in the length of the experiment it was necessary to provide the chamber with facilities for feeding, watering, and the collection of excreta. These additions to the respiration chamber are shown in Fig. 2.

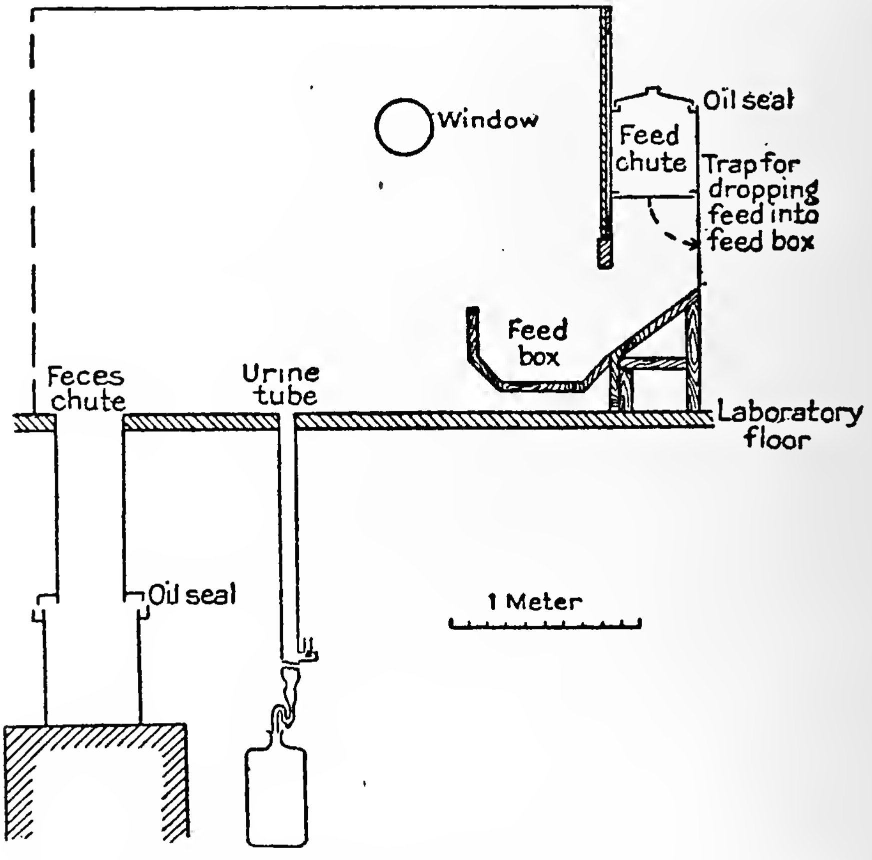

FIG. 2.—Feed-chute, feed-box, feces-chute, and provision for collection of urine in respiration chamber

Provision for feeding—Feed is introduced through a metal chute or feed-box of galvanized iron, firmly riveted and soldered to the front wall of the chamber. It is provided with a cover, which fits into an oil-seal, and with a trap-door, hinged on the front wall of the chamber. By means of this trap-door the upper half of the feed-chute may be entirely closed off from the lower half, the object being to prevent a rapid exchange of air from the respiration chamber when the cover on top of the chute is momentarily removed and feed is inserted. When the trap-door is open it hangs suspended by the hinges. Two flexible wires (picture-cord) connected with the trap-door pass through the side walls of the chamber, and the trap may be closed from the outside, without removing the cover of the feed-box, by pulling on the wires until the door forms a firm contact with the projecting flanges, shown in Fig. 2. The holes through which the wires are passed are waxed, to prevent leakage of air. The bottom of the feed-chute slopes toward the feed-box at an angle of about 45°, so that the feed slides down into the feed-box within easy reach of the animal. The bottom of the feed-box is reenforced on the outside with matched wooden sheathing, supported by four legs. This gives somewhat more stability and also eliminates the possible pull which would otherwise be exerted by this additional weight on the front of the chamber wall. The feed-box itself is built of matched sheathing, snugly fitted against the inside wall of the chamber, so that the front bevel or slope of the box is continuous with the sloping floor of the feed-chute.

Provision for water—The device for watering consists of a heavy, sheet-metal tank, 9 inches wide, 20 inches long, and 8 inches deep, with a rounded bottom. (See *c*, Fig. 1.) The water is introduced through a short pipe attached to the bottom at the rear of the tank. This pipe is connected with an opening in the side-wall of the chamber by means of rubber tubing, a glass water-gage (through which the water is siphoned into the tank) being attached to the outside of the chamber and connected with this opening. The water-tank itself is attached at a convenient height on the outside of the feed-box toward the room containing the absorber table, so that the water can be supplied from the outside at any time without breaking the air-seal of the chamber. The water-gage is connected with the opening in the side of the chamber by a piece of rubber tubing, which forms a **U**-curve below the level of the water-tank, so that the tank can be completely drained and there will still be sufficient water in the tube to act as a seal against passage of air.

Swivel stanchion—The original, rigid stanchion was replaced by a modern steel swivel stanchion such as is used in dairy barns. This gives the animal somewhat more liberty of movement and makes it easier for it to reach the water-tank, which is placed at one side of the feed-box.

Provision for collection of urine—Although the respiration experiments during the long fasts of 5 to 14 days were only of 2 hours' duration, it was desirable to collect all the urine without loss during the entire progress of the fast, and provision was therefore made for the collection of the urine voided while the animal was inside the chamber. The collection of urine is relatively simple when the animals are in the metabolism stalls, but is more complicated when they are in the respiration chamber, because of the necessity for preventing any leak in the air-seal of the chamber. At the beginning of the experimental series the urine voided in the chamber was collected through a brass pipe attached to the side of the chamber. The end inside the chamber was connected with the urine-funnel by a piece of garden-hose. To the end outside a piece of rubber tubing was attached, the other end of the rubber tubing being inserted into a bottle containing a water-seal. In the experiments beginning early in the fall of 1922, the following method has been used in collecting the urine: A heavy brass tube, 4 inches in diameter and 4 feet long, provided at one end with a flange about 1½ or 2 inches in width, is projected down through a hole in the floor of the chamber, with the flange resting on the inside of the metal floor of the respiration chamber. This tube is held firmly in place in part by the flooring (7.6 cm. thick), through which it passes, and in part by 3 lag screws or bolts 2 inches in length, by which the flange of the tube is screwed to the floor. The edges of the flange are soldered, as are also the heads of the screws, to insure against leakage of air. This tube is just long enough to allow for the raising and lowering of the hose inside of it connecting with the urine-funnel. Only a short piece of hose is used, which is weighted with lead at the bottom to take up the slack when the animal lies down. The tube leading out of the chamber consists of two parts. The upper section, extending downward from the floor of the chamber, is of ordinary 4-inch tubing, fitted at the bottom with a small valve through which water can be passed to the inside of the water-seal. The lower section consists of a piece of ¾-inch brass pipe, curved to give a water-seal, and provided at the upper end with a brass cone which gradually widens out to 4 inches so as to fit against the upper part of the urine-tube. The two sections are firmly held together by a piece of automobile inner tubing of stout rubber, fastened on with clamps. The size of rubber tubing most suitable for this purpose is that which will require some stretch when put around the metal tubes, so that the closure will be air-tight. The urine, as collected, flows out of the brass tube into an appropriate container below. With this arrangement it is possible to collect the urine throughout the entire day. Prior to its installation, the complete 24-hour collection of urine could only be made if the animal was kept standing all the time. This apparatus for the collection of urine while the steer is in the chamber has functioned satisfactorily.

Provision for collection of feces—The arrangement for collecting feces consists of a chute, as shown in Fig. 2. This chute is made of galvanized sheet metal. Its width dimensions are 3 feet by 1 foot, and it extends 3 feet below the bottom of the floor of the chamber. The top is soldered to the inside of the metal floor of the chamber. The bottom is provided with a flange projecting horizontally 4 inches from the four walls of the chute. The outside edges of this flange have a 2-inch perpendicular drop, which fits into the oil-seal of the large metal container for collecting the feces. The top of the chute is covered with a heavy iron grid, to prevent the animal from stepping down into the opening. This grid is flush with the floor of the chamber (see *d*, Fig. 1), but is 4 inches lower than the platform upon which the animal rests. During an experiment the feces container is pushed up tightly against the feces-chute, so that the inside wall of the oil-groove fits closely against the horizontal flare of the chute, thus preventing the feces from dropping into the oil-seal. As shown in Fig. 2, the oil-seal has been broken and the container has been lowered several inches to secure clearance for removal.

CHANGES IN THE TECHNIQUE FOR MEASURING THE RESPIRATORY EXCHANGE

Soda-lime

As a result of the development of the many forms of respiration apparatus used for clinical purposes, chiefly for humans, there have been placed upon the market several kinds of soda-lime which are claimed to be much superior to that regularly used in the Durham apparatus. Their relative merits need not be discussed here, but it should be pointed out that practically all of these newer types of soda-lime contain relatively large amounts of water and therefore should not be used with this respiration chamber. The soda-lime used in the Durham apparatus contains a minimum amount of water.[a] The technique for preparing it has been described in earlier publications.[b]

Determination of Proportion of Air Escaping Through Openings in Wind-chest.

The wind-chest on the absorber table has three air outlets, two each 10 mm. in diameter and the third 97 mm. The air discharged through one or both of the 10-mm. openings may be directed through the absorption system and its carbon-dioxide content determined, but the air passing through the 97-mm. opening is discharged into the laboratory room. With this arrangement, which was modeled directly after the original aliquoting device described in a previous publication,[c] simultaneous measurements of the carbon-dioxide production may be made by directing the air from both 10-mm. openings through duplicate sets of absorbers. But in the experiments with fasting steers duplicate collections of carbon-dioxide were not made, and hence the air from only one of the 10-mm. openings was passed through the absorption system, the air from the other 10-mm. opening being discharged into the room. By reducing the size of the 97-mm. opening with different disks having openings of different sizes, the amount of the aliquot passing through the 10-mm. opening into the absorption system may be varied, as explained in detail in our earlier publication.[d]

The disk factor, or the relative proportion of air discharged into the absorption system, remains constant even with relatively large fluctuations in the rate of ventilation. Recent experimental work indicates, however, that during the respiration experiment itself it is better to maintain always the *same rate of ventilation as that under which the disk factor was established,* i. e., the discharge into the wind-chest should be reasonably constant.

The escape of air from the wind-chest is obviously dependent on the pressure inside the wind-chest. This is equivalent to but a few millimeters of water pressure, and yet changes in pressure inside the wind-chest do produce disturbances in the relative discharges through the various orifices. When variations occur in the disk factor with the same disk, it is because

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[a] This soda-lime can be secured through Mr. W. E. Collins, 555 Huntington Avenue, Boston, Massachusetts, or through Stanley Jordan & Co., 93 Water Street, New York City.

[b] Atwater and Benedict, Carnegie Inst. Wash. Pub. No. 42, 1905, p. 29; also, Benedict, Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1924, Abt. IV, Teil 10, p. 449.

[c] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, p. 103.

[d] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 61.

of changes of air pressure in the wind-chest. Furthermore, in order to secure uniformity and invariability in the size of the aliquot from period to period or from experiment to experiment, the air discharged into the sampling can with rubber-diaphragm top must always be discharged against atmospheric pressure. This pressure, which must remain neutral, is indicated by an oil manometer.

The best method of establishing the disk factor is, first, to set the apparatus in motion as for an experiment. The respiration chamber must then be ventilated until it contains only pure, outdoor air. A known quantity of carbon dioxide is then discharged into the system through a small rubber tube, inserted directly into the pipe at some point between the wind-chest and the blower inside the respiration chamber which forces air into the wind-chest. Formerly it was recommended that the carbon dioxide be discharged into the intake side of this blower. The prime requisite in this procedure is that *all* the carbon dioxide should be discharged into the wind-chest without first permeating the atmosphere of the chamber. In a standard carbon-dioxide test the gas is diffused directly into the respiration chamber and the carbon dioxide in the residual air in the chamber is determined by analysis. In the disk-factor test, however, any carbon dioxide escaping back into the chamber would involve an error. Consequently, the carbon dioxide should be introduced at a point between the blower and the wind-chest, as the chance of leakage into the chamber is thus practically eliminated. Indeed, it may be introduced into the same pipe outside of the respiration chamber, if desired. Subsequent weighing of the absorption vessels, with due allowance for the carbon dioxide in the normal outdoor air, indicates what proportion of the total amount of carbon dioxide introduced has been delivered into the sampling-can and from there passed through the absorption system.

TABLE 6.—*Proportion of air (disk factor) discharged through absorption system according to the size of openings in wind-chest*

Diameter in mm. of openings in wind-chest	Disk factor
	p. ct.
10, 10, and 29	10.20
10, 10, and 16	22.84
10[1] and 16	27.00
10, 10, and 50	3.84

[1] The other 10-mm. opening was plugged with a rubber stopper.

With the introduction and measurement of carbon dioxide in the absorption system under the above conditions, disk factors have been established according to the different disks used in the 97-mm. opening, and for different rates of ventilation. These disk factors are tabulated in Table 6. The disk factor can of course be approximately established by determining the relative area of the three openings in the wind-chest, but this is not so accurate a measure as the method just described.

Selection of Disk Opening to Meet Specific Experimental Requirements

In any experimental period the minimum amount of carbon dioxide absorbed should be not less than 4 grams, as the unavoidable error in weighing the large absorbers approaches closely to 1 per cent when the absorbers have increased in weight only 4 grams. On the other hand, when the air-flow through the absorbers is high, so that a very large amount of carbon dioxide is absorbed in any given period, the amount of water-vapor carried over from the soda-lime into the sulphuric-acid bottle is also correspondingly large. As it has been found that the particular type of sulphuric-acid bottle which may be conveniently used has an efficient maximum absorbing capacity of 10 grams of water-vapor, this imposes indirectly a maximum limit to the amount of carbon dioxide that can be absorbed. Between these two extremes, therefore, one must carefully choose the size of the disk opening to meet the conditions of the experiment.

The object in varying the size of the aliquot is mainly to direct a sufficient proportion of the total air through the absorbers, so that the amount of carbon dioxide absorbed, regardless of the length of period, will be within the limits of error that might be introduced in weighing it. Thus, for small animals, and also for animals which are fasting or on submaintenance rations and which give off small amounts of carbon dioxide, a small disk opening which gives a higher disk factor, i. e., a larger aliquot, should be used. When the experimental periods are short, the aliquot should be a larger proportion of the total amount of air than when they are long. In the 24-hour experiments, in which the individual periods were 8 hours long, use was made of a 50-mm. disk, which resulted in an aliquot representing only 3.84 per cent of the total discharge of air. Thus it was possible not to exceed the maximum absorbing capacity of the soda-lime and sulphuric-acid bottles, even in a period as long as 8 hours.

Gas-analysis Apparatus

Importance of Gas Analysis

The aliquoting device used in connection with the respiration chamber for steers provides for the exact determination of the carbon dioxide removed by the ventilating air-current, but it does not indicate the change in the carbon-dioxide residual in the chamber during the experimental period. In computing from the carbon dioxide in the aliquot the total carbon-dioxide production, correction must be made, however, for any change in the residual carbon dioxide. In short half-hour periods this correction is particularly essential, if the total carbon-dioxide production is to be determined accurately. In periods as long as 24 hours any changes in the residual carbon dioxide might be disregarded without introducing too great an error in the final calculations, but this procedure is not recommended. For the determination of the change in residual carbon dioxide a small Haldane apparatus for carbon dioxide only was originally used.

In addition to the measurement of the residual carbon dioxide, gas analysis has another use. In fasting experiments, in which the nutritive state is so profoundly affected, it becomes necessary to know more accurately the character of the food or of the body material burned. To obtain this end the respiratory quotient must be determined, since it serves as an admirable index of the nature of the material being katabolized. Thus, the higher the quotient the larger the proportion of carbohydrates being burned, and conversely, the lower the quotient the nearer the approximation to a pure-fat combustion. The respiratory quotient is therefore of value in interpreting the rate of change in the character of the metabolism during the course of the fasting period and likewise in the subsequent feeding period. Perhaps the most important use of the respiratory quotient, however, in these experiments was to provide a truer indication of the calorific value of carbon dioxide, which should be employed in computing heat by indirect calorimetry from the carbon-dioxide measurements. The calorific value of carbon dioxide ranges from 6.694 to 5.047 calories per liter, depending upon whether the combustion is pure fat or pure carbohydrate. If the respiratory quotient is actually determined, then it becomes unnecessary to assume an average respiratory quotient or to employ the otherwise indispensable carbon dioxide to heat ratios determined by Armsby, Fries, and Braman.[a]

With the original set-up of the respiration chamber for steers it was possible to measure only the carbon-dioxide production. When the carbon-dioxide production and the respiratory quotient are both known, however, the computation of the oxygen consumption of the animal is relatively simple, and from this latter value the calculation of the heat-production is most exact. This is the main purpose of gas analysis in connection with this respiration chamber. The direct determination of the oxygen consumption of large animals, such as steers, is difficult, because the ventilating air-current in the respiration chamber must be large. Obviously, the closed-circuit principle, which has been so successfully employed with humans, would be impracticable, both on account of the complexity of the apparatus and because of the large amount of oxygen which must be directly supplied in a closed-circuit apparatus. Only with the Zuntz apparatus[b] has an attempt thus far been made to determine directly the oxygen consumed by the animal. An application of the principle simultaneously set forth by Jaquet[c] in Basel and Hasselbalch[d] in Copenhagen seemed advisable. To secure a gas-analysis apparatus, however, that would function perfectly and indicate with great exactness the relatively small percentage differences in the carbon-dioxide increment and in the oxygen deficit was a problem of no small magnitude. Experience in the Nutrition Laboratory with the Sondén gas-analysis apparatus[e] left nothing to be desired, save that the apparatus is not portable and can not be shipped safely.

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[a] Armsby, Fries, and Braman, Proc. Nat. Acad. Sci., 1920, **6**, p. 263. These factors give the ratio of carbon dioxide to heat for cattle, as determined in their respiration calorimeter under definite feeding conditions, and we found them invaluable in the interpretation of our results on undernutrition.

[b] Zuntz, Landw. Jahrb., 1909, **38**, Ergb.-Bd. 5, p. 473; also Zuntz, VIII. Internat. Physiol. Kongress, Wien, Sept. 1910. For further details see also Zuntz, Jahrb. d. deutsch. Landw.-Gesellschaft, 1912, **27**, p. 180, and Umschau, No. 5, Jan. 1911; also Zuntz, Von der Heide, and Klein, Landw. Versuchs-Stationen, 1913, **79–80**, p. 806; ibid., Landw. Jahrb., 1913, **44**, pp. 776 et seq.

[c] Jaquet, Verhandl. Naturf. Gesellsch., Basel, 1904, **15**, p. 252.

[d] Hasselbalch, Respirationsforsøg paa nyfødte Børn, Bibliotek for Laeger, Copenhagen, 1904, **8**, p. 219.

[e] Benedict, Carnegie Inst. Wash. Pub. No. 166, 1912.

Description of Gas-Analysis Apparatus

A practical gas-analysis apparatus of portable type having the desired accuracy was, therefore, developed by Dr. T. M. Carpenter, of the Nutrition Laboratory. This apparatus represents the principle of the Haldane apparatus applied to the determination both of the percentage of oxygen and of carbon dioxide in the air sample, and it combines the highly desirable

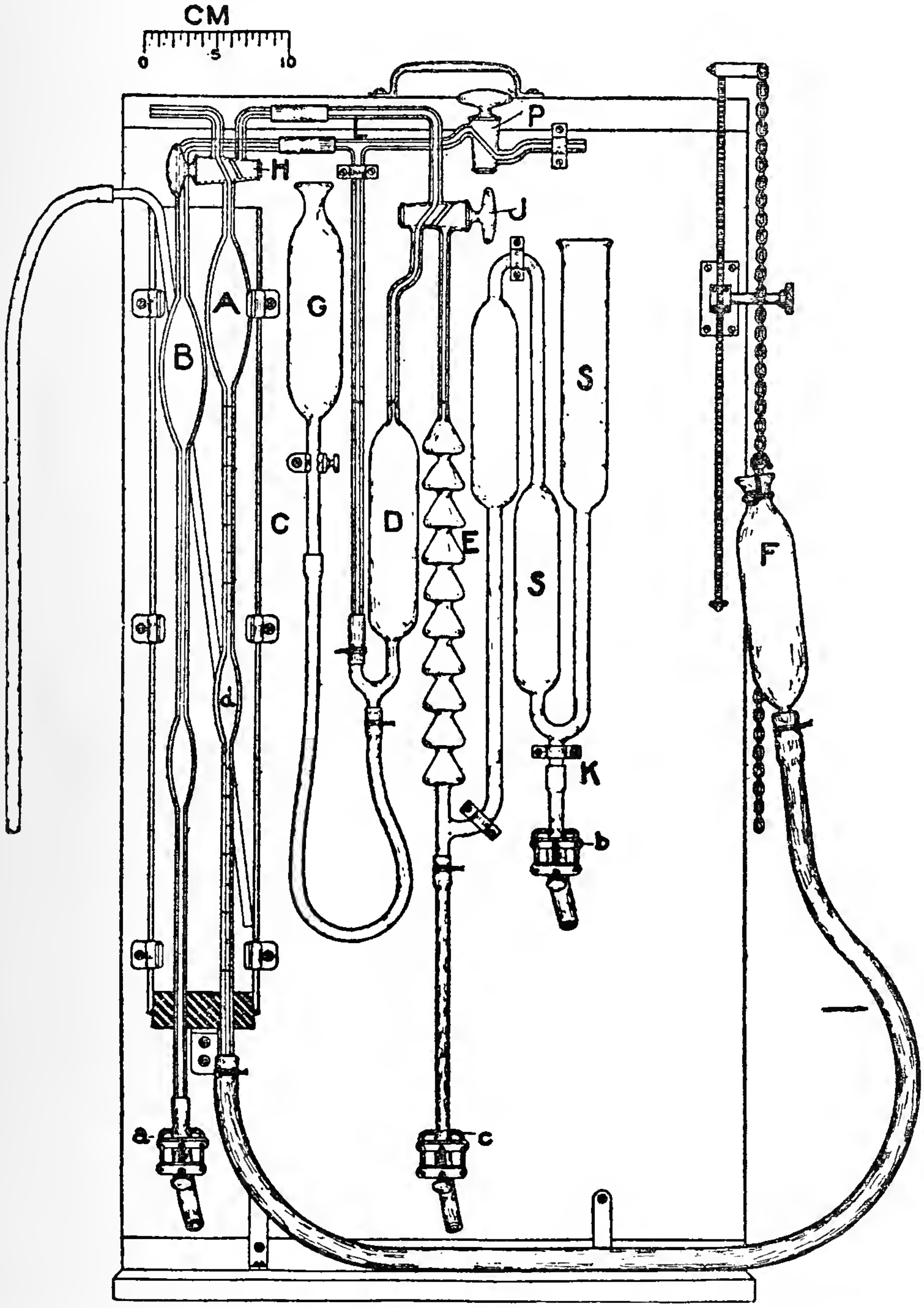

Fig. 3.—Diagram of Carpenter apparatus for exact analysis of atmospheric and chamber air

The burette *A*, with its smaller bulb *d*, and the compensator *B*, are immersed in water in the container *C*. Intercommunication between the burette and the carbon-dioxide absorption pipette *D* and the oxygen absorption pipette *E* is secured by taps *H* and *J*, and between the compensating bulb *B* and the pipette *D* by the capillary tee *L*. The tap *P* provides for preliminary adjustment to the open air. *F* is a mercury leveling-bulb for the burette *A*, and *G* is a leveling-bulb for the pipette *D*. *SS* is a water reservoir, with outlet *K*, to protect solution in *E* from air and serve as a pressure medium. Pinch-cocks *a*, *b*, and *c* provide for introduction or withdrawal of liquids.

features of great accuracy and of transportability. One of its outstanding characteristics is its facility of manipulation. This apparatus has already been described in detail by Dr. Carpenter.[a] Its importance in respiration experiments of the type reported in this monograph and its general adoption in several laboratories justify the presentation here, however, of the diagrammatic sketch of the apparatus. (See Fig. 3.) The details of the method of calibration and manipulation will be found in the two earlier publications describing the apparatus.[a] The accuracy of the apparatus is controlled frequently by determinations of the carbon dioxide and oxygen in samples of outdoor air, since the composition of outdoor air has been established as constant.[b]

THE PHYSIOLOGICAL CONTROL OF GAS-ANALYSIS APPARATUS

The gas-analysis apparatus of Dr. Carpenter has been extensively controlled by analyses under conditions where ethyl alcohol is being burned in a closed chamber and the theoretical respiratory quotient for alcohol is found. But in respiration experiments of the character reported in this monograph the metabolism of the animal itself serves as an automatic check of the apparatus, since after the first few days of fasting one would expect an approximation to a pure-fat combustion, with a respiratory quotient but a little over 0.70. To use the actual respiratory quotient determined for an animal as a proof of the accuracy of the gas-analysis apparatus would not, of course, be legitimate under any conditions save during fasting. But the fasting animal itself furnishes an excellent control of the determinations of the respiratory exchange in a respiration apparatus. Thus, the Nutrition Laboratory has for many years used respiratory quotients determined on fasting geese as a test of the accuracy of various forms of respiration apparatus. Fortunately, the first extensive application of the Carpenter gas-analysis apparatus occurred in a series of fasting experiments, in which it could be assumed that the katabolism closely approximated a pure-fat combustion. It will be observed in a later section of this monograph (see pp. 157 to 161) that the trend of the respiratory quotient in all the fasting experiments corresponded exactly to that which one would theoretically expect with a fasting animal.

INSTALLATION OF THE GAS-ANALYSIS APPARATUS AT DURHAM AND CORRECTION IN CALCULATION OF CARBON-DIOXIDE PRODUCTION NECESSITATED BY ITS USE

In the earlier experiments with this respiration chamber only the carbon-dioxide content of the air inside the chamber was determined, a small Haldane apparatus being used for the purpose. After the development of the exceedingly accurate Carpenter apparatus, the air leaving the chamber was analyzed to determine both the carbon-dioxide increment and the oxygen deficit created by the animal. Indeed, such analyses were made in most of the experiments reported in this monograph. An air sample may be taken at the exact beginning or end of a period, either by means of the well-

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[a] Carpenter, Journ. Metabolic Research, 1923, 4, p. 1; see, also, Benedict, Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1924, Abt. IV, Teil 10, p. 628.

[b] Benedict, Carnegie Inst. Wash. Pub. No. 166, 1912.

known Haldane gas-sampler or by means of the sampler designed by Bailey.[a] When gas samples are to be stored and subsequently analyzed, the Bailey sampler is the better. It is important at this point to emphasize that the gas-samplers, as well as the mercury itself, must be dry, and the air, if it is to be stored, should be sampled after passing through sulphuric acid and therefore dry, for when moist samples are stored for 12 or more hours there is invariably a loss of carbon dioxide.[b] In our case, however, analyses were made continuously and samples were rarely stored.

The gas-analysis apparatus was set up in a room adjoining that in which the absorber table was placed, an air sample being conducted from the absorber table to the gas-analysis apparatus by means of a ¼-inch metal pipe. Sufficient pressure to insure a steady flow of air was easily secured by tapping the pipe conducting the air from the positive blower to the absorbers at a point near the blower, this being the point of highest pressure. The samples used for analysis contained the normal amount of moisture[c] in the chamber atmosphere, as they were taken before the air passed through the first sulphuric-acid container. Two pet-cocks in series were employed to regulate the air-current going to the gas-analysis apparatus. One was set open permanently, just wide enough to allow the proper amount of air to flow through the sampling-tube to the gas-analysis apparatus; the other was used as a shut-off. Hence the amount of air thus passing through the tube was dependent solely upon the length of time the pet-cock was open.

In using the apparatus, the shut-off was opened exactly 2 minutes before the end of the period, allowing the air to flow to the gas-analysis apparatus. At the exact end of the experimental period this pet-cock was shut off and the time the valve had been opened was noted with a stop-watch. Obviously the amount of air thus diverted from the aliquot to the gas-analysis apparatus carried with it carbon dioxide, which was diverted from absorption in the soda-lime bottles. Since the air was analyzed, however, by volumetric analysis, it was only necessary to determine the volume diverted during the time the valve had been open, from which one could easily compute the amount of carbon dioxide lost from the aliquot. This volume was accurately measured for different rates of ventilation with a small gas-meter placed at the outlet of the sampling-tube. A table of factors was then drawn up, showing the volume of air flowing through the sampling-pipe for the varying lengths of time that the pet-cocks had been open. Since the rate of flow through the sampling-pipe changed very little, whether the ventilation-rate of the sampling current was 24 or 36 cubic feet per half hour, the average of the different rates of ventilation between these limits was taken as a constant in preparing the table of factors. The amount of carbon dioxide computed from the volume of air passing through the sampling pipe and the determined percentage of carbon dioxide was added to the weight of carbon dioxide collected in the absorbing vessels, prior to the calculation of the total amount of carbon dioxide produced during the experimental period.

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[a] Bailey, Journ. Lab. and Clin. Med., 1921, 6, p. 657; ibid., Journ. Biol. Chem., 1921, 47, p. 281.

[b] Benedict, Carnegie Inst. Wash. Pub. No. 166, 1912, pp. 106 et seq.

[c] When samples are to be stored, they must be taken dry, preferably in a Bailey sampler, and taken at a point between the sulphuric-acid bottles and the soda-lime bottle, i. e., usually from a pet-cock in the pipe rising through the table and conducting air to the soda-lime bottles.

PROCEDURE FOR MOST ACCURATE DETERMINATION OF RESPIRATORY QUOTIENT

When it is desired to determine the respiratory quotient with great accuracy, the carbon-dioxide increment and the oxygen deficit should be large, as the possible error involved in the gas-analysis is thereby, theoretically at least, reduced. Hence, in these experiments, as a matter of safeguard, it was aimed to establish a high content of carbon dioxide (circa 1 per cent) in the air of the chamber just before the beginning and just after the end of the experiment and to determine the respiratory quotient from these highly saturated samples. This condition was obtained by leaving the animal in the chamber approximately one hour without ventilation. Respiratory quotients were also determined throughout the experiment, but not with such a high carbon-dioxide content of the chamber air. With small animals or animals on submaintenance rations or fasting, the carbon-dioxide production per half hour is very low, and in such cases this procedure for determining the respiratory quotient accurately becomes a necessity.

PRINCIPLES UNDERLYING CONTROL TESTS OF RESPIRATION CHAMBER BY ADMITTING KNOWN AMOUNTS OF CARBON DIOXIDE

The importance of making frequent tests of the operating efficiency of the apparatus can not be over-emphasized. The general principle of conducting gas checks has already been described.[a] At least two procedures are possible. In the first place, the respiration chamber may be thoroughly ventilated with outdoor air and carbon dioxide may then be introduced into the chamber more rapidly than it is withdrawn. At the end of a half hour (the length of an ordinary period) one can weigh the carbon dioxide accumulated in the soda-lime bottles, correct for the normal carbon-dioxide content of the air entering the soda-lime bottles, correct for any carbon dioxide diverted in the air sample going to the gas-analysis apparatus, and finally, compute from the disk factor the total amount of carbon dioxide that has left the respiration chamber. The final value thus obtained must, in this particular case, be increased by a large corrective factor due to the accumulation of carbon dioxide inside the chamber. Indeed, when the air of the chamber is of outdoor composition at the start, this correction factor may represent three-fourths or more of the total amount of carbon dioxide introduced. Obviously, therefore, this particular type of gas-check would test the accuracy of the gas-analysis apparatus (i. e., the determinations of the residual carbon dioxide) and the measurement of the volume of the chamber to a much greater extent than it would the accuracy of the mechanical aliquoting device and of the absorption system. Indeed, a test of the chamber might be made with a very low ventilation-rate, so that the carbon dioxide would accumulate inside. In such a test the rotary blower discharging air from the chamber would be maintained at a speed only sufficiently high to preclude any back diffusion of air out of the loosely sealed door. Under these conditions it would be possible to carry out a test in which 90 per cent of the carbon dioxide introduced would accumulate in the chamber. Such tests have, as a matter of fact, actually been carried out, and are usually successful.

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 70 et seq.

The second ideal method is to have the rate of ventilation and the introduction of carbon dioxide so nearly balance that the residual carbon dioxide would be the same at the end as at the beginning of the period. Under these conditions there would be no correction for the residual carbon dioxide, and the test becomes purely a test of the mechanical aliquoting device and the absorption of carbon dioxide. This second method is believed to be the best. It necessitates, however, an accumulation of the carbon dioxide in the air of the chamber prior to the true test to a point at which the relationship between addition and removal can be held constant during the subsequent test. The point will obviously vary with the amount of carbon dioxide introduced per half hour. The amount per half hour should, theoretically at least, closely approximate the amount which will probably be produced by the animal under study. Indeed, gas-checks are usually made with this chamber under conditions which closely represent those produced by the animal under investigation.

TABLE 7.—*Typical calculation of a 4-hour carbon-dioxide check test*
(12^{h}04^m p. m. to 4^{h}05^m p. m., March 26, 1924)

Weight of absorbing vessels at end....grams..	5,777.85
Weight of absorbing vessels at start.... do. ..	5,761.10
CO_2 absorbed from aliquot of outgoing air.... do. ..	16.75
Volume of aliquot of outgoing air....cubic feet...	123.0
CO_2 in aliquot from outdoor air[1] (1.23 × 1.6)....grams..	1.97
CO_2 in aliquot from chamber (16.75 − 1.97).... do. ..	14.78
CO_2 in air escaping through valve.... do. ..	0.09
Total CO_2 in aliquot from cylinder (14.78+0.09).... do. ..	14.87
CO_2 in total outgoing air[2] $\left(\frac{14.87 \times 100}{3.84}\right)$.... do. ..	387.24
Residual CO_2 in chamber at end.... p. ct...	0.331
Residual CO_2 in chamber at start.... do. ..	0.030
Change in residual CO_2.... do. ..	0.301
Change in residual CO_2 corrected[3] (0.18×0.301×1,000)....grams..	54.18
CO_2 corrected by residual (387.24+54.18).... do. ..	441.42
Weight of steel cylinder at start.... do. ..	1,402.55
Weight of steel cylinder at end.... do. ..	961.40
CO_2 admitted to chamber.... do. ..	441.15
Per cent CO_2 withdrawn from chamber $\left(\frac{441.42 \times 100}{441.15}\right)$....p. ct...	100.06

[1] Estimated that each 100 cubic feet of outdoor air contains 1.6 grams carbon dioxide.

[2] 3.84 equals percentage of total outgoing air actually passing through absorption system, i. e., when the 10, 10, and 50 mm. openings are used. (See Table 6, p. 30.)

[3] Estimated that each 0.001 per cent carbon dioxide corresponds to 0.18 gram carbon dioxide, as the volume of air in the chamber is about 9,000 liters.

In connection with the 24-hour experiments having periods of 8 hours' duration, a gas-check extending over 4 hours was made. For this test the disk with the 50-mm. opening was used in the larger aperture in the wind-chest, the disk factor for which had been established to be 3.84 per cent. The results of such a test are tabulated in Table 7.

ANIMALS USED IN EXPERIMENTS

Our first extensive research with ruminants was made with 14 steers in groups of from 2 to 5 animals.[a] The uniformity of results shown between the individuals in each group, both on maintenance and on submaintenance feed-levels, indicated that two well-selected animals would be sufficient for a study of fasting, provided they do not vary materially in age, breeding, and conformation. If in any experiment, however, two similar animals do not give approximately the same result, then the particular factor under investigation should be studied with a larger group. Accordingly, most of the work on fasting was carried out with two adult steers (C and D), each weighing about 600 kg. These animals were reasonably close duplicates of two of the large, full-grown steers (A and B) studied in the research on undernutrition. In order to study the influence of size and age on fasting metabolism, a pair of steers about 12 months of age (E and F) were likewise secured. The animals in each pair were essentially physiological duplicates. Thus, to a certain extent each experiment was carried out in duplicate, each pair of animals receiving absolutely the same treatment with regard to environmental temperature, feed, and general handling.

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923.

GENERAL PLAN OF RESEARCH

FASTING ON DIFFERENT PLANES OF NUTRITION

Since the fundamental problem under investigation was to determine the influence of fasting upon the physiological behavior of beef steers, particular attention was centered on a study of the respiratory exchange, the heat-production, and the composition of the urine. The nutritive plane upon which the animals were living before the fast was purposely altered, to determine the influence that such differences in the nutritive level would exert on the well-known drafts upon the body organism for maintenance of life during subsequent fasting. Thus, several fasts were carried out with steers C and D in a well-nourished condition, that is, after they had been gaining flesh for some time. In four instances the feed-level previous to fasting was approximately maintenance. In two instances steers C and D were subjected to fasting after having been on pasture for several months, when they were in a condition approximating that of animals in wild life, having a water-rich fill of green grass, the flesh being soft, and the body more or less water-logged. They also fasted after a fairly prolonged period upon submaintenance rations, consisting of approximately one-half of the usual caloric intake necessary for maintenance. Since the changes occurring in the animal organism during the first two or three days of fasting are most profound, the effect of repeated 48-hour periods of fasting with weekly intervals of refeeding was studied, to secure added information on this point. Steers E and F were likewise studied during fasting after submaintenance feeding, and with them a special study was made comparing the metabolism during 2 days on feed with that during 2 subsequent days of fasting. In this series maintenance and submaintenance feed-levels were contrasted, and the relative effects of timothy and alfalfa hay were also studied. The experimental series did not include fasting experiments at the height of fattening.

SUBSIDIARY PROBLEMS

Undernutrition—Since these fasting experiments followed different nutritive planes, each pair of steers was fed on submaintenance rations previous to one fast, and further data were thus secured on the influence of undernutrition upon the metabolism of steers, which supplement the findings in the earlier report on undernutrition.[a]

Reaction to ingested food after fasting—The effect of the ingestion of food on metabolism was determined from various standpoints. In the first place, observations were made of the effect of the first feed after fasting, when the stomach was practically devoid of any food. With steers C and D the metabolism was also measured under the regular conditions of feeding, over periods lasting from 2 to 8 hours. In these cases the animal was put into the respiration chamber immediately after having consumed a regular feed. Of greater importance was a series of continuous four-day respiration experiments with steers E and F, in which the influence of the ingestion of

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923.

food was studied during a period of 2 days of regular feeding immediately followed by 2 days of fasting.

Environmental temperature—Our earlier research[a] suggested that the metabolism of ruminants occasionally decreases with a falling temperature, a phenomenon at variance with all popular conceptions and previous investigation on this subject. In the experimental series beginning in January 1923, therefore, it was planned to include a study of the effect of environmental temperature on metabolism. Wide ranges in temperature were purposely selected, and the metabolism of the animals was measured at these different temperatures, both while they were fasting and while they were on different feed-levels, including maintenance and submaintenance.

Body position—The importance attached to the influence of standing and lying upon the metabolism of ruminants has brought forth considerable discussion on the subject, resulting in the recomputation of much previously published work.[b] It seemed desirable, therefore, to supplement our earlier, rather fragmentary findings.[c] As it is a habit of cattle not to lie down for a very long period at a time, it is unfortunately impossible to measure the metabolism during a long period of lying only. The problem is not so difficult when the steers are standing, as they can readily be forced to stand. A few observations of the metabolism with the steer in the lying and standing positions were made during the period of this research. These were supplemented by others made during the winter of 1925–26. From these later results it becomes apparent that the subject demands a far more critical investigation than was at first anticipated. Therefore we do not feel justified at the time of sending this manuscript to the printer (summer of 1926) in discussing this important problem, since our data are as yet by no means complete.

Insensible loss—Throughout this research records were kept in 24-hour periods of the body-weight, the amounts of feed and water consumed, and the weights of feces and urine excreted. The data are therefore available for computing the daily insensible loss of each of these four steers during the entire experimental season, both when they were fasting and when on feed. These data furnish new material in the study of the physiology of ruminants which was not obtained in our earlier research on undernutrition.[d] In view of the close correlation between the insensible loss and the metabolism already noted with humans,[e] it was considered advisable to determine whether this correlation also exists with ruminants and how it is affected by fasting as compared with different feed-levels.

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 219 and 301.

[b] Fries and Kriss, Am. Journ. Physiol., 1924, **71**, p. 60.

[c] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 215.

[d] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 85.

[e] Benedict, Bull. Soc. Sci. d'Hygiène Alimen., 1923, **11**, p. 357; ibid., Schweiz. med. Wochenschr., 1923, **53**, p. 1101; ibid., The correlation between perspiratio insensibilis and total metabolism, Collection of articles dedicated to the 75th birthday of Prof. I. P. Pawlow, published from the Institution of Experimental Medicine in Leningrad, 1924, p. 193; also, Benedict and Root, Arch. Intern. Med., 1926, **38**, p. 1.

CHRONOLOGY OF THE FASTING RESEARCH

The first fasting experiment was designed as a general exploratory measure, to discover how steers would react when completely deprived of food, since the opinions with regard to the probable outcome were greatly diversified. The general plan of the research as a whole rapidly shaped itself at the conclusion of the first fast, and a series of fasts of 5 to 14 days, as well as a series of 2- and 3-day fasts, were successfully carried to completion with steers C and D. Later the factor of age was introduced with two younger steers (E and F), and the plan of research was enlarged to include continuous 4-day respiration experiments. A chronological list of the fasting experiments is given in Table 8, in which the length of the fast represents the time between the last feed given before the fast and the first feed given after the fast. The fasting experiments with steers E and F between December 1924 and May 1925 represent in each case a continuous 2-day sojourn in the respiration chamber without food, immediately preceded by a continuous 2-day respiration experiment during which the steer received feed (maintenance or submaintenance rations) at the usual hours.

TABLE 8.—*Chronological list of fasting experiments*

Steer and date of last feed	Length of fast[1]		Steer and date of last feed	Length of fast[1]		Steer and date of last feed	Length of fast[1]	
Steer C:	*days*	*hrs.*	Steer D:	*days*	*hrs.*	Steer E:	*days*	*hrs.*
Dec. 6, 1921	7	9	Dec. 6, 1921	7	9	Feb. 12, 1924	5	3
Jan. 4, 1922	10	10	Jan. 4, 1922	10	10	Apr. 8, 1924	4	2½
Apr. 17, 1922	14	7½	Apr. 17, 1922	14	7½	Dec. 14, 1924	2	9
June 1, 1922	6	1½	June 1, 1922	5	4	Jan. 14, 1925	3	1
Nov. 6, 1922	10	1	Nov. 6, 1922	8	3	Feb. 3, 1925	3	1
Jan. 3, 1923	3	3½	Jan. 9, 1923	3	4	Mar. 1, 1925	2	9
Jan. 15, 1923	2	..	Jan. 17, 1923	2	3	Mar. 18, 1925	2	9
Jan. 21, 1923	2	4	Jan. 25, 1923	2	3½	Apr. 15, 1925	2	9
Jan. 28, 1923	2	4	Feb. 1, 1923	2	1½	May 5, 1925	2	23
Feb. 5, 1923	2	3½	Feb. 8, 1923	2	4			
Feb. 11, 1923	2	4	Feb. 14, 1923	2	3½	Steer F:		
Feb. 18, 1923	2	3½	Feb. 22, 1923	2	3½	Feb. 12, 1924	6	2½
Mar. 1, 1923	2	3½	Mar. 5, 1923	2	4½	Mar. 31, 1924	4	2½
Mar. 8, 1923	2	3½	Mar. 13, 1923	2	3½	Dec. 19, 1924	2	9
Mar. 15, 1923	2	3½	Mar. 20, 1923	2	3½	Jan. 20, 1925	3	1
Mar. 22, 1923	2	3½	Nov. 4, 1923	4	22	Feb. 13, 1925	3	1
Nov. 4, 1923	5	19	Mar. 3, 1924	9	3	Mar. 25, 1925	2	9
Mar. 3, 1924	10	3½	May 13, 1924	4	2	Apr. 22, 1925	3	1
Apr. 22, 1924	4	2	Nov. 11, 1924	2	..	May 12, 1925	3	1
Nov. 11, 1924	2	..						

[1] Length of fast signifies time between withholding of feed and resumption of feeding.

DETAILS OF THE EXPERIMENTAL CONDITIONS

Continuous daily records were kept throughout the entire experimental season each year of the body-weight, weights of drinking-water and feed, and weights of urine and feces. From these data it has been possible to compute the daily insensible perspiration. In addition, daily records were also made of the temperature of the drinking-water, the temperature of the metabolism stalls in which the animals were kept, the rectal temperature, and the heart-rate. Various body measurements were made periodically, but only the chest circumference was recorded daily, since it was believed that this is the best single measurement indicative of any change in flesh or organized body-tissue.

The routine observed in securing the body-weights was as follows: At exactly 2 p. m. each day the same steer was led onto the scales and weighed. He was then given water to drink from a tub, and again weighed and put into the stall, and the next steer was weighed in like manner. The tub of water was weighed before and after each animal drank, the decrease in weight representing the weight of water consumed and also serving as a check on the measurement of the body-weight, since the increase in body-weight should agree with the decrease in weight of the tub. Beginning with November 11, 1924, the body-weights were taken at $4^h 30^m$ p. m. instead of at 2 p. m. These weights, in fact all records except chest circumference, heart-rate, and body temperatures, were checked by a second observer.

Native hay, comprising at least 75 per cent of timothy hay, was given to all four steers from November 1921 until March 1925, when alfalfa hay was fed. The meal mixture given to the adult steers, C and D, consisted of a mixture of equal parts by weight of corn meal, linseed meal, and wheat bran. The young steers, E and F, however, were given a mixture of equal parts by weight of linseed meal and wheat bran, without the corn meal, the object being to promote growth.

During the periods of maintenance feeding all four steers received hay twice each day, i. e., at $4^h 30^m$ p. m. and at 8 a. m. The meal mixture during the feeding-period from November 26, 1921, to December 6, 1921, was given only once each day, at 7 a. m., but thereafter during maintenance feeding it was given twice daily, at 7 a. m. and about $3^h 30^m$ p. m. in the case of all four steers. During the submaintenance period in the spring of 1923, steers C and D were fed hay twice each day, that is, one bag containing 4.5 kg. of hay was fed during the 24 hours, approximately one-half of the bag being given in the late afternoon and the rest on the following morning. No meal was given to steers C and D at this time. In the case of steers E and F, in the submaintenance period in 1923–24, hay was fed only once daily, i. e., in the morning, and meal in the late afternoon. In the submaintenance period in 1924–25, however, these steers received hay in the afternoon only and no meal at all. No meal was fed to steers C and D after June 23, 1923, or to steers E and F after April 18, 1924.

The 24-hour periods for the collection of data for all 4 steers began and ended at 2 p. m. during the experimental season from November 1921, through May 1924, except for the fast in March 1924, with steers C and D, when the day began and ended at 7 a. m. In November 1924, and thereafter through the winter and spring of 1925, the daily periods were begun and ended at $4^h 30^m$ p. m.

OBSERVATIONS ON MATURE STEERS C AND D

Steers C and D were purchased and brought to the agricultural experiment station at Durham, New Hampshire, on October 26, 1921. According to the statement of the farmer from whom they were purchased, these steers were at that time about 3½ years of age. They were both predominantly of Shorthorn breeding, but steer C showed a trace of some other blood by his black muzzle. After their arrival they were kept in temporary quarters until November 26, 1921, when the metabolism stalls were completed in the laboratory for animal nutrition. Their first feed in the metabolism stalls was given at $4^h 30^m$ p. m., November 26, 1921, and thereafter the regular routine of procedure, as already outlined, was carried out. A supply of hay rations was weighed out for a month in advance, and samples were taken for analysis, but the meal ration was weighed out daily. The feed refused was removed and weighed before the next 24-hour feeding-period began, and a record was kept of the exact amount uneaten.

Fasting experiments were made with both steers on December 6 to 13, 1921, and January 4 to 14, 1922. During the period between February 2 and March 21, 1922, steers C and D had to be kept in temporary quarters again, owing to a fire in the laboratory and the time required for repairs, so that the daily records could not be secured.

Details of the 14-Day Fast in April 1922

A complete picture of a fast can be obtained only from records which indicate the physiological condition of the animal before the fast, during the fast, and during recuperation. It seems inadvisable to incur the expense which would be involved in publishing the huge amount of data representing in detail all these various physiological levels. Accordingly, although in the discussion of results the detailed data secured during the progress of each fast will be given in the various tables, the complete daily data for the periods prior to and following the fast are given only for the 14-day fast. (See Tables 9 and 10.) The various recuperation periods following the fasts which did not exceed 5 to 7 days were rapid and similar, and present nothing unusual which would warrant the expense involved in publishing in detail the extensive data secured during these periods. During the longer 10- and 14-day fasts, however, the recuperation was much slower and the data for the refeeding period following the 14-day fast are therefore given in detail.

In Tables 9 and 10 the dates when respiration experiments were made are indicated by asterisks. The experiments in the respiration chamber were usually made in the morning and in all cases where the "standard metabolism" (see p. 228) was to be measured the afternoon feed of the day prior to the experiment and the morning feed on the day of the experiment were withheld, so that the animal might be studied at least 24 hours after eating. The body-weights and weights of water recorded in these two tables were secured at 2 p. m. The measurements of the chest-girth were taken just before the steer was weighed. The data for water, feed, excreta, and insensible loss represent total amounts for 24-hour periods, beginning at 2 p. m. on the given date. The containers for the excreta, both feces and urine, were removed at 2 p. m., i. e., immediately after weighing the animal, so that the weights of excreta are those amounts actually voided between 2 p. m. of one day and 2 p. m. of the next day.

The fast in April 1922 was begun after the steers had been on a constant ration of hay and meal for 17 days, i. e., since March 31, 1922. An exami-

Table 9.—*Statistics of experiment of April 17 to May 1, 1922, steer C*

Date	Body-weight		Chest-girth	Water		Feed[1]		Excreta		Insensible loss	Stall temp.
	Total	Change		Total	Temp.	Hay	Meal	Feces	Urine		
1922	*kg.*	*kg.*	*cm.*	*kg.*	*°C.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*°C.*
Apr. 10...	602.8	+ 4.2	201	35.6	12	8.98	3.00	26.57	4.35	17.8	22
Apr. 11...	601.6	− 1.2	201	32.2	12	8.90	3.00	25.60	4.39	13.0	13
Apr. 12...	602.8	+ 1.2	201	32.0	12	8.92	3.00	23.30	4.22	13.0	13
Apr. 13...	606.2	+ 3.4	201	33.8	11	8.96	3.00	26.31	4.58	14.2	18
Apr. 14...	606.8	+ 0.6	202	32.8	13	8.94	3.00	23.08	4.03	17.2	21
Apr. 15...	607.2	+ 0.4	201	34.4	13	8.94	3.00	23.20	4.65	15.4	17
Apr. 16...	610.2	+ 3.0	198	33.6	15	8.77	3.00	26.38	4.54	16.6	20
Apr. 17*..	608.2	....	198	32.0	14	0.00	0.00	20.43	5.25	12.6	20
Apr. 18*..	602.0	− 6.2	199	12.4	14	0.00	0.00	7.08	7.72	6.0	20
Apr. 19*..	593.6	− 8.4	198	4.6	14	0.00	0.00	4.82	5.26	7.2	20
Apr. 20*..	581.0	−12.6	196	0.0	13	0.00	0.00	3.95	3.16	2.4	15
Apr. 21*..	571.4	− 9.6	197	3.8	13	0.00	0.00	2.91	2.03	3.2	20
Apr. 22*..	567.0	− 4.4	196	9.6	17	0.00	0.00	3.35	3.84	4.2	22
Apr. 23*..	565.2	− 1.8	196	0.2	14	0.00	0.00	2.25	2.18	3.8	22
Apr. 24*..	557.2	− 8.0	196	4.4	20	0.00	0.00	3.22	1.92	3.6	22
Apr. 25*..	552.8	− 4.4	196	3.2	17	0.00	0.00	1.28	2.09	4.0	23
Apr. 26*..	548.6	− 4.2	194	4.6	18	0.00	0.00	0.69	2.12	4.8	20
Apr. 27*..	545.6	− 3.0	194	5.2	18	0.00	0.00	2.60	4.63	2.0	22
Apr. 28*..	541.6	− 4.0	193	0.0	19	0.00	0.00	1.21	2.01	3.0	21
Apr. 29*..	535.4	− 6.2	193	2.2	19	0.00	0.00	1.14	1.61	3.6	21
Apr. 30*..	531.2	− 4.2	193	4.8	17	0.00	0.00	0.92	2.35	3.4	21
May 1*..	529.4	− 1.8	193	1.8	16	3.79	0.00	0.85	0.97	4.0	19
May 2...	529.2	− 0.2	193	15.4	16	4.46	0.00	2.38	1.71	6.6	22
May 3...	538.4	+ 9.2	193	24.4	17	7.31	0.00	7.08	2.47	7.0	19
May 4...	553.6	+15.2	193	20.2	15	7.33	0.00	13.73	2.49	6.2	14
May 5...	558.8	+ 5.2	193	21.4	16	7.18	0.00	15.48	2.26	7.4	19
May 6...	562.2	+ 3.4	196	20.6	13	8.36	0.00	18.56	2.90	8.0	19
May 7...	561.8	− 0.4	194	32.8	18	8.13	0.00	20.13	2.72	8.0	18
May 8...	571.8	+10.0	196	20.6	13	0.00	0.00	18.86	3.78	5.2	18
May 9*..	564.6	− 7.2	193	0.6	16	8.98	4.00	13.11	3.09	10.4	21
May 10...	551.6	−13.0	193	31.0	15	8.31	4.00	16.70	4.03	12.6	21
May 11...	561.6	+10.0	193	32.2	15	6.96	4.00	20.02	3.04	13.2	19
May 12...	568.6	+ 7.0	193	36.0	12	8.42	4.00	22.60	2.87	14.6	20
May 13...	577.0	+ 8.4	196	35.8	12	8.24	4.00	24.41	3.17	15.0	19
May 14...	582.4	+ 5.4	196	35.8	12	8.58	4.00	26.06	3.23	17.0	20
May 15...	584.4	+ 2.0	196	38.6	13	8.93	4.00	25.98	3.82	17.4	20
May 16...	588.8	+ 4.4	196	39.2	14	8.84	4.00	26.54	4.62	15.2	17
May 17...	594.4	+ 5.6	197	37.8	14	8.83	4.00	29.87	4.48	14.6	17
May 18...	596.0	+ 1.6	198	39.2	15	8.65	4.00	32.43	7.94	15.4	17
May 19...	592.0	− 4.0	197	38.2	13	8.95	4.00	27.50	7.13	17.8	20
May 20...	590.8	− 1.2	196	39.2	13	8.70	4.00	32.58	3.26	18.8	22
May 21...	588.0	− 2.8	196	38.6	13	8.96	4.00	30.08	3.54	20.4	24
May 22...	585.6	− 2.4	196	38.8	13	8.92	4.00	27.92	4.08	16.4	22
May 23...	589.0	+ 3.4	196	39.4	15	8.95	4.00	26.98	4.62	16.8	20
May 24...	593.0	+ 4.0	196	40.8	14	8.99	4.00	28.18	4.40	16.4	21
May 25...	597.8	+ 4.8	197	37.4	13	8.98	4.00	25.10	4.47	17.6	22
May 26...	601.0	+ 3.2	198	39.2	12	8.87	4.00	28.81	4.56	16.6	21
May 27...	603.2	+ 2.2	199	39.6	14	8.92	4.00	27.59	5.18	14.0	16
May 28...	609.0	+ 5.8	199	35.0	14	8.99	4.00	29.34	6.57	17.2	22
May 29...	603.8	− 5.2	199	38.6	13	8.92	4.00	29.31	5.61	18.4	24
May 30...	602.0	− 1.8	201	38.8	12	7.62	3.97	31.96	4.97	16.6	22
May 31*..	598.8	− 3.2	199	40.2	15	8.91	4.00	26.61	4.71	16.8	23
June 1*..	603.8	+ 5.0	......	......	......	......	......	......	......	......	......

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[1] 50 gm. salt also eaten on April 12 and 16, and May 2, 6, 10, 19, 23, and 29

TABLE 10.—*Statistics of experiment of April 17 to May 1, 1922, steer D*

Date	Body-weight		Chest-girth	Water		Feed[1]		Excreta		Insensible loss	Stall temp.
	Total	Change		Total	Temp.	Hay	Meal	Feces	Urine		
1922	*kg.*	*kg.*	*cm.*	*kg.*	° *C.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	° *C.*
Apr. 10...	614.6	+ 0.8	208	31.4	12	8.96	3.00	21.62	4.49	15.4	22
Apr. 11...	616.4	+ 1.8	208	29.6	12	8.82	3.00	22.29	4.54	11.6	13
Apr. 12...	619.4	+ 3.0	208	29.4	12	8.84	3.00	24.26	4.92	12.8	13
Apr. 13...	618.8	− 0.6	208	31.8	12	8.86	3.00	22.65	4.68	14.2	18
Apr. 14...	621.0	+ 2.2	208	31.8	15	8.92	3.00	22.23	4.88	15.0	21
Apr. 15...	622.6	+ 1.6	208	31.8	15	8.94	3.00	22.34	4.75	13.2	17
Apr. 16...	626.0	+ 3.4	208	29.6	13	8.90	3.00	22.26	5.50	15.8	20
Apr. 17*..	624.0	....	210	32.4	15	0.00	0.00	19.06	5.71	12.4	20
Apr. 18*..	619.2	− 4.8	206	7.8	13	0.00	0.00	7.42	6.73	4.2	20
Apr. 19*..	608.6	−10.6	206	8.4	14	0.00	0.00	5.47	6.98	5.2	20
Apr. 20*..	599.4	− 9.2	203	5.2	13	0.00	0.00	3.81	3.20	4.2	15
Apr. 21*..	593.4	− 6.0	203	0.0	......	0.00	0.00	1.42	2.43	3.0	20
Apr. 22*..	586.6	− 6.8	203	7.8	17	0.00	0.00	2.54	2.29	3.8	22
Apr. 23*..	585.8	− 0.8	203	0.0	......	0.00	0.00	1.81	1.57	3.6	22
Apr. 24*..	578.8	− 7.0	203	6.8	19	0.00	0.00	1.39	1.87	3.8	22
Apr. 25*..	578.6	− 0.2	202	4.8	17	0.00	0.00	1.32	1.92	4.6	23
Apr. 26*..	575.6	− 3.0	202	8.4	18	0.00	0.00	1.25	7.65	3.4	20
Apr. 27*..	571.8	− 3.8	203	0.0	......	0.00	0.00	1.33	2.32	3.2	22
Apr. 28*..	565.0	− 6.8	203	6.8	19	0.00	0.00	1.39	3.81	2.8	21
Apr. 29*..	563.8	− 1.2	201	4.4	19	0.00	0.00	1.08	5.68	4.2	21
Apr. 30*..	557.2	− 6.6	201	0.0	......	0.00	0.00	0.63	1.90	2.8	21
May 1*..	551.8	− 5.4	201	0.0	......	3.75	0.00	0.70	1.16	4.8	19
May 2...	548.8	− 3.0	201	11.2	17	3.51	0.00	0.93	1.92	5.0	22
May 3...	555.6	+ 6.8	201	20.6	17	5.52	0.00	3.18	3.98	5.4	19
May 4...	569.2	+13.6	203	12.2	14	5.51	0.00	7.33	4.22	4.4	14
May 5...	571.0	+ 1.8	201	10.6	17	6.34	0.00	10.45	2.34	5.8	19
May 6...	569.4	− 1.6	203	14.0	16	7.02	0.00	12.96	3.25	7.2	19
May 7...	567.0	− 2.4	202	24.8	17	8.92	0.00	14.19	3.00	6.6	18
May 8...	577.0	+10.0	203	19.0	15	0.00	0.00	16.86	2.53	5.6	18
May 9*..	571.0	− 6.0	202	6.4	16	8.85	4.00	13.33	3.07	9.8	21
May 10...	564.0	− 7.0	201	32.0	15	7.86	4.00	17.32	4.00	12.2	21
May 11...	574.4	+10.4	203	34.8	14	7.69	4.00	19.98	3.28	11.8	19
May 12...	585.8	+11.4	203	27.0	14	7.84	4.00	24.05	3.13	13.0	20
May 13...	584.4	− 1.4	203	35.0	21	7.78	4.00	23.09	3.51	13.6	19
May 14...	591.0	+ 6.6	203	31.8	15	8.10	4.00	24.58	4.43	15.2	20
May 15...	590.6	− 0.4	203	32.8	14	8.86	4.00	23.36	5.62	14.4	20
May 16...	592.8	+ 2.2	203	37.6	15	8.69	4.00	25.57	4.76	13.0	17
May 17...	599.8	+ 7.0	203	32.4	15	8.06	4.00	26.37	4.31	11.8	17
May 18...	601.8	+ 2.0	203	31.0	14	8.97	4.00	24.35	4.48	13.8	17
May 19...	603.2	+ 1.4	203	35.8	15	8.48	4.00	25.23	5.83	14.2	20
May 20...	606.2	+ 3.0	206	33.2	14	8.71	4.00	26.16	5.31	14.0	22
May 21...	606.6	+ 0.4	206	33.8	15	8.64	4.00	26.35	4.92	18.8	24
May 22...	603.0	− 3.6	203	37.2	16	7.81	4.00	31.10	4.09	14.8	22
May 23...	602.0	− 1.0	206	35.0	15	8.89	4.00	29.23	4.70	14.6	20
May 24...	601.4	− 0.6	206	37.0	15	8.25	4.00	28.09	3.75	14.6	21
May 25...	604.2	+ 2.8	206	39.4	15	7.82	4.00	30.35	3.47	15.6	22
May 26...	606.0	+ 1.8	206	37.0	15	8.76	4.00	28.32	3.81	14.2	21
May 27...	609.4	+ 3.4	208	37.2	13	8.93	4.00	28.18	3.91	12.6	16
May 28...	614.8	+ 5.4	206	36.2	14	8.72	4.00	29.68	4.81	15.4	22
May 29...	613.8	− 1.0	206	36.0	15	7.68	4.00	28.31	5.78	16.6	24
May 30...	610.8	− 3.0	206	38.6	15	8.40	4.00	28.01	4.73	14.2	22
May 31*..	614.8	+ 4.0	206	35.6	13	7.22	4.00	28.96	5.52	15.8	23
June 1*..	611.4	− 3.4	......	......	......	......	......	......	......	......	......

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[1] 50 gm. salt also eaten on May 2, 6, 10, 19, 23, and 29.

nation of the detailed records in Tables 9 and 10 shows that from the beginning of the fast on April 17 there was a steady, pronounced loss in weight with both animals, which persisted throughout the entire fast. The water intake also fell off noticeably, the animals occasionally refusing to drink at all. The decrease in the daily weight of feces was fairly uniform. The volume of urine fluctuated considerably, although the general average shows a similar decrease. The insensible loss dropped noticeably after withholding of feed, but with the resumption of feeding it gradually regained a high level. The stall temperature remained reasonably constant throughout the entire period from April 10 to June 1. The chest circumferences showed characteristic decreases during the fasting period and a slow increase subsequently, although on the first of June, at the end of the refeeding period, the chest circumference of neither animal had returned to its original magnitude.

Steer D recuperated much more slowly on the ration of hay only than did steer C after this 14-day fast. During the first 7 days, when hay alone was fed, he ate nearly 1 kg. less per day than did steer C and showed much less inclination to eat. During the 23 days following, when both hay and meal were fed, he ate less hay daily than did steer C, and although he cleaned up the meal every day, he left the general impression that he was much slower in regaining his normal vigor than steer C. Certainly he did not gain as much during the month of recuperation after the 14-day fast as did steer C, which made remarkable progress in so short a time. It is evident, therefore, that the recuperative capacity of steer D was somewhat below that of steer C.

Both steers had regained their original prefasting weight and vigor by June 1, and both were in excellent condition for the fourth fast. Judged on the basis of general appearance and so-called "handling," they were both in a higher state of flesh than they had been at any previous time since they were purchased. Steer C had made an especially rapid improvement during the month of refeeding. He took on flesh rapidly and carried a good covering of flesh. In live weight he had almost overtaken steer D, which had weighed 16 kg. more at the beginning of the fast. Steer D also had taken on considerable flesh and looked in excellent condition, but his total increase in weight was not so large as that of steer C.

During the last 6 days of this fast, records were kept of the time spent standing and lying during each 24-hour period.

General Observations During the 14-Day Fast

The first feed withheld was the afternoon feed on April 17. Both animals were placed in the respiration chamber on this date, steer C in the morning and steer D in the afternoon, but since both had been fed about $6^h\ 30^m$ a. m., the measurements do not represent standard metabolism. At feeding-time (about 4 p. m.) on April 17, steer D was very noisy and restless, but steer C was somewhat less active.

On the morning of April 18, at approximately $5^h\ 30^m$ a. m., about 50 grams of the urine of steer C were lost. Both animals were much quieter on the morning of April 18, steer D lying down much of the time. On April 18 steer C was in the respiration chamber from shortly after 9 a. m. until

$12^h 25^m$ p. m. He was weighed and watered as usual at 2 p. m. Steer D was studied in the respiration chamber on the afternoon of April 18.

During the afternoon of April 18, steer C was very restless in the stall, continually lying down and rising. When lying, he kicked and lowed spasmodically. These symptoms (supposedly of colic) started shortly after he was watered at 2 p. m. and continued until $5^h 45^m$ p. m., when he lay down and became quiet for the rest of the evening. The continuous effort of rising and lying down, together with the apparent colic, seemed to weaken him somewhat, as he was very relaxed during the rest of the night.

About 4 a. m. on April 19, steer C urinated while lying down. This was the first time in our experience that an animal had urinated while lying, and it suggested that the steer felt too weak to rise. Some urine was unavoidably lost, as a consequence. The rectal temperature during this period of colic was normal, but the volume of urine passed was almost double the normal amount. On April 19, both animals behaved normally, although steer C still showed signs of fatigue, especially after coming out of the respiration chamber, when he lay down immediately and remained in this position practically all the afternoon.

Both steers were remarkably quiet and inactive up to the third day of fasting, April 20, except for the first afternoon, April 17, and to a less extent during the second day, April 18. They had not shown any particularly pronounced anxiety for feed, as indicated by restlessness or lowing, and certainly showed no distress. On the sixth day of fasting, April 23, they were still doing well, with no signs of distress or other disturbance.

The feces of both animals were still fairly firm on the fourth day, April 21, but the amounts were becoming markedly smaller. On the seventh day, April 24, the feces of steer C were somewhat softer. During the evening, between 6 p. m. and $8^h 30^m$ p. m., he passed from 15 to 20 grams of material rather solid in form, reddish in appearance, and resembling tissue, slightly bloody, and mixed with mucus. The assistant on watch reported that he strained considerably in passing this. The material was extremely offensive in odor. Steer D behaved as usual.

On the eighth day, April 25, the feces of steer C were very loose, but there was no change in rectal temperature and, so far as could be seen from general observation, he was very bright and acted as usual. No change was noted with steer D.

On the ninth day, April 26, steer C behaved as usual, being quiet and alert. The feces of steer D were becoming loose or soft at this time, while those of steer C were becoming firm and pilular again, although they were not exceedingly dry. Both animals still rose from the lying position with apparent ease, showing no signs of weakness or of having to exert particular effort in rising. In lying down, however, they relaxed more suddenly after they were nearly down than they did when on feed. This was noticed with steer C, especially after his attack of colic on the second day, from which he seemed otherwise to have entirely recovered. This relaxation on the part of the steers after they were nearly down was probably in part due to the narrowness of the stalls, which gave them less opportunity to spread their legs.

During the morning of the tenth day, April 27, steer D urinated for the first time while lying down, and approximately 100 grams of urine were spilled.

Both animals acted somewhat stiff on April 28, and hunched their backs somewhat when led from the stalls to the respiration chamber. Their gait was slightly unsteady, perhaps due to weakness. The consistency of the feces varied with different defecations, being sometimes very soft. Those of steer C were soft when voided in the chamber, a fact which suggests a possible influence of the exertion of prolonged standing.

There was no unusual behavior of the steers on April 29. On the evening of April 29, i. e., after 12 days of fasting, tests of the acidity of the urine were begun, on the supposition that the steers had reached a carnivorous condition and were living on their own body-tissue, and that their urine should consequently give an acid reaction to litmus paper rather than the characteristic alkaline reaction of the urine of herbivora.

Both steers were in the respiration chamber on the morning of May 1, the fourteenth day of the fast, and at 2 p. m. the fast ended. Steer C was weighed, fed 1,810 grams of hay, and put into the chamber again immediately after eating. The respiration experiment was continued from 4 p. m. until approximately 10 p. m., the purpose being to note the change in the respiratory quotient and to measure the rise in the carbon-dioxide production which follows the ingestion of food.

Summarized Details of Other Fasts of Steers C and D

Steers C and D were subjected to their fourth fast on June 1–7, 1922, and at 10 a. m. on June 10, 1922, they were turned out to pasture. Here they remained until November 6, 1922, when a fasting experiment after pasture feeding was made. They were brought to the laboratory at 8 a. m., November 6, 1922, after having had their last feed on pasture that morning, and the fasting period began at once. Both steers were in better condition of flesh at the beginning of this fast than they had been at any time since they were purchased. Steer C was especially well fleshed; in fact, he weighed approximately 100 kg. more than at the start of any previous fast. Steer D weighed about 75 kg. more than he had prior to the previous fasts. This excess in weight, however, probably did not entirely represent organized body-tissue, but in part liquid mass of fill, due to the green feed.

Between January 3 and June 5, 1923, steers C and D were subjected to a series of intermittent fasts of from 48 to 72 hours in length. During the intervals between these short fasts until March 28 a constant daily ration of 9 kg. of hay and 2 kg. of meal was given. During this time steer C was subjected to 11 and steer D to 10 fasts. Between March 28 and April 25 the daily ration for both steers consisted of 9 kg. of hay only. After April 25 the ration was reduced to 4.5 kg. of hay until June 5 for steer C and June 7 for steer D, when the ration was again increased to 9 kg. of hay, which level was maintained until June 22. A special feature of these short fasts was a study of variations in environmental temperature, with a view to determining if extremes in temperature would alter the metabolism materially.

Both steers were turned out to pasture at $12^h\ 20^m$ p. m., June 23, 1923. On June 22, before going to pasture, steer C weighed 666.4 kg. and steer D weighed 637.4 kg. The animals were brought back to the barn again on October 31, 1923, and placed in a small pasture adjoining it for 4 days. Between 3 and 4 p. m., November 4, 1923, they were placed in stalls in this barn, without feed, preparatory to respiration experiments beginning on the morning of November 5. At 8 a. m., November 5, they were brought to the metabolism laboratory and weighed, steer C weighing at this time 735.6 kg. and steer D 717.2 kg. They were weighed again at 2 p. m., November 5, and the collections of feces and urine for the 5-day fasting period were begun at this time.

After their fast in November 1923, steers C and D were again removed from the metabolism stalls to the barn, where each was fed regularly 9 kg. of hay per day until December 21. On this date the daily ration for each animal was reduced to 4.5 kg. (i. e., a 50 per cent maintenance ration) and continued at this level through the morning feed of March 3, 1924, when the steers were subjected to a 10-day fast. This reduction in feed was made for the specific purpose of placing these animals upon the same submaintenance ration as was given to steers A and B in the earlier research, with the idea of studying the effect of a fast following a reasonably prolonged period of undernutrition. On February 25, 1924, steers C and D were moved from the barn to the metabolism stalls, where the collection and aliquoting of feces could again be made. This allowed one complete week before the fasting began in which they could become adjusted to the difference in temperature and the greater restriction of the metabolism stalls. The urine and feces were, as usual, collected in 24-hour periods. The daily periods were from 2 p. m. to 2 p. m. until March 3. March 3–4 was only a 17-hour day, when the feces and urine were collected from 2 p. m., March 3, to 7 a. m., March 4. On March 4 and thereafter throughout this fast the animals were weighed and watered at 7 a. m. daily, so that two separate collections of feces and urine, representing separate day and night periods, could be made.

The study of the respiratory exchange and the energy transformations in the fasts between November 1921 and March 1924 was based upon a series of relatively short respiration experiments. Many of the experiments on ruminants by earlier investigators have been made in respiration chambers or calorimeters in which the experimental periods were 24 hours in length. Consequently, with steers C and D an experiment was made in April and May 1924, respectively, in which each animal remained inside the respiration chamber for 3 days continuously. Unweighed amounts of drinking-water were allowed, as desired, a tub being placed in the chamber for this purpose and water being introduced through a short piece of rubber tubing connecting the tub with the outside of the chamber. No attempt was made to determine the amount of urine and feces passed. The time was too short to bring these animals back to first-class condition for these fasts. They had come in from pasture the preceding November, full of green grass and in excellent condition. They were then given a one-half maintenance ration for the better part of the winter, after which they fasted for 10 days. At the end of this fast, when each animal had lost on the average not far from 40 kg., they were each fed 9 kg. of hay daily, steer C until April 22, when he fasted for 4 days, and steer D until May 13, when he also fasted for 4 days. At the beginning of the 10-day fast in March, which followed the long period of submaintenance feeding, steer C weighed on the average about 635 kg. and steer D 622 kg. At the beginning of his 3-day respiration experiment on April 23, 1924, steer C weighed 669.6 kg., and at the beginning of his 3-day respiration experiment on May 14 steer D weighed 664.6 kg., i. e., each weighed from 35 to 40 kg. more than at the end of the submaintenance period on March 3. It is highly improbable that with but 9 kg. of hay per day in a period of 5 or 8 weeks the entire loss during 10 days of fasting could have been made up by each animal. It is more likely that this increase in weight represented largely increase in fill or in the contents of the alimentary tract, due to doubling the quantity of the ration and thus automatically the water intake.

The chest circumference of steer C at the beginning of the March fast was 208 cm., and it was the same on April 22, prior to the 4-day fast. The chest circumference of steer D measured 212 cm. before the March fast and 210 cm. before the May fast. This measure of the condition of flesh of steer C would indicate complete recuperation back to the point of beginning the 10-day fast in March. This would not be entirely true of steer D, whose chest circumference was actually 2 cm. less (indicating less flesh), although his weight had increased 40 kg. Under these circumstances it seems probable that steers C and D were in a condition more nearly approximating undernutrition than a normal condition.

No records of insensible loss were kept during the feeding period following the fast in March 1924, or during the fasts in April and May 1924.

Steer C was in the respiration chamber continuously from $7^h 45^m$ a. m., April 23, 1924, to $7^h 45^m$ a. m., April 26, 1924, and steer D was in the chamber continuously from $7^h 36^m$ a. m., May 14, 1924, to $7^h 36^m$ a. m., May 17, 1924, each animal having been without food for 24 hours before entering the chamber. While in the chamber the animals were allowed to lie or stand at will. Careful records were obtained with regard to the amount of time spent standing and lying. These records have an important bearing upon the interpretation of the measurements of the metabolism during the individual experimental periods, which were of 8 hours' duration at this time instead of the usual 30 minutes. As a general index of the total 24-hour metabolism of animals under conditions of stall confinement, these 8-hour periods present, theoretically at least, a much more perfect picture than do short half-hour periods.

No records of feed consumed after these 4-day fasts were kept, and on May 19, 1924, the steers were turned out to pasture.

In connection with an experiment to determine the insensible loss under extremely varying conditions of feeding, both steers again fasted for 2 days each, on November 11 and 12, 1924. This was the last fast conducted with these steers. The steers had been on pasture since May 19, 1924, and had been brought off pasture on the morning of November 11, 1924.

OBSERVATIONS ON IMMATURE STEERS E AND F

In addition to the study of the effect of fasting upon adult steers on various nutritive planes, it seemed advisable to study the influence of fasting upon young, growing animals, which presumably would react to the lack of food more acutely than adult animals. To make the experiment still more critical, it was proposed to place these younger animals upon a distinctly submaintenance ration, so that they would begin their fast in a condition of undernutrition. This preliminary preparation, therefore, became part of a subsidiary study of the effect of undernutrition upon young steers.

Two young, purebred, Shorthorn steer calves, E and F, were purchased in the fall of 1923. Both were born on November 28, 1922. They had been kept in an ordinary lot, where they ran loose with a dozen other calves. On October 13, 1923, the day they were delivered at the laboratory in Durham, steer E weighed 288.0 kg. and steer F weighed 310.8 kg. Previous to their arrival they had been fed a ration of hay and silage, with a small amount of grain, which provided for ordinary growth. They were consequently in a good, vigorous, and thrifty condition and in a fair state of flesh, but carried no great amount of fat.

The 24-hour periods for collection of data began and ended at 2 p. m. in the case of these steers, for all dates from the beginning of the experimental season in November 1923, through April 1924. The 24-hour periods in the fall and winter of 1924–25, however, began and ended at 4^h 30^m p. m.

When steers E and F arrived at Durham, they were placed at first in temporary quarters, but on November 14, 1923, they were taken to the metabolism stalls. From this date until December 17, 1923, they received an approximately maintenance ration, consisting of 5 kg. of hay and 0.68 kg. of meal daily. From December 17, 1923, to February 12, 1924, they were fed a submaintenance ration of 2.5 kg. of hay and 0.30 kg. of meal, the amount of meal being reduced to 0.10 kg. on January 28. On February 12, 1924, they began a 5-day and 6-day fasting experiment, respectively, under the usual conditions prevailing in the previous fasts, except that steers E and F started their fast on a submaintenance plane of nutrition. Prior to this fast the "standard metabolism" (see p. 228) of both animals was studied at intervals of approximately one week, both upon the maintenance and submaintenance levels of nutrition. Special consideration will be given to these data subsequently. (See pp. 228 to 234.)

In addition to the 3-day respiration experiments during the April and May fasts of steers C and D, steers E and F were also subjected to a continuous 3-day respiration experiment while fasting. On February 29, 1924, following a short period of readjustment after the February fast, both animals were placed on a daily ration of 5 kg. of hay and 0.91 kg. of meal. This feed-level was continued until March 31 with steer F and until April 8 with steer E, when each animal was subjected to a 4-day fast. Daily records of live weights, weights of urine and feces, and records of the insensible loss were not obtained previous to and during these fasts, as the main object was a study of the respiratory exchange.

At the beginning of these particular fasts the body-weights of steers E and F were not far from those when they were first received at the laboratory, although they were nearly 5 months older and would normally have gained in weight. Thus, the body-weight of steer E was 280 kg. on April 9, 1924, as compared with an initial weight on November 19, 1923, of 266.2 kg., and that of steer F was 295.2 kg. on April 1, 1924, as compared with an initial weight of 291 kg. The body-weights in April, therefore, represent a thinner state, more nearly approaching the condition of undernutrition. The steers had been fed more hay and meal after the fast in February 1924, however, than they had received during November and December 1923, that is, 5 kg. of hay and 0.91 kg. of meal per day as compared with the earlier so-called "maintenance" ration of 5 kg. of hay and 0.68 kg. of meal. That they had fully made up all their losses during the period of undernutrition, and particularly during the 5-day fast in February, and at the same time had made up for growth is highly improbable. These animals were therefore undoubtedly in a distinctly undernourished state in April. Their chest circumferences in April 1924 were essentially the same as those at the time of their purchase, but notably greater than during the period of undernutrition. The estimate of the nutritive plane of these animals is complicated by the fact that they were growing, but the general conclusion is that although not in a good state of flesh, they were not so thin in April as in February, at the beginning of their longer fasts.

At the end of his fast, on April 12, 1924, steer E weighed 260.8 kg., having lost 19.2 kg. in the 4 days of fasting. Steer F weighed 271.8 kg. at the end of his fast on April 4, 1924, having lost 23.4 kg. The chest circumference of steer E was 145 cm. prior to fasting and 142 cm. for several days following the fast, but by April 18 it was again 145 cm. The chest circumference of steer F was 150 cm. before the fast and 147 cm. after the fast, but was again 150 cm. on April 18.

Between December 1924 and May 1925 a series of continuous 4-day respiration experiments were made with steers E and F, with the object of studying the method of estimating the fasting metabolism from the effect of quantitative variation of the same feed. These respiration experiments consisted of 2 days when the animal received feed, followed by 2 days of fasting. For at least 2 weeks prior to each experiment and during the first 2 days in the respiration chamber the feed-level was held constant, either at maintenance or submaintenance. The effect of high and low environmental temperatures and the relative difference in the effect of timothy and alfalfa hay were also studied. During the two weeks preceding each 4-day respiration experiment careful records were kept daily of the measurements necessary for the computation of the insensible loss. Chemical analyses of the urine and feces were not made, however. While the steer was in the chamber the feces were collected only at the end of the 4 days, as it seemed more important not to break the air-seal of the respiration chamber than to have a daily record of the weights of feces. It was possible in most instances, however, to secure the daily weights of urine voided, and samples were taken for nitrogen determinations.

RECORDS OF LAST INDIVIDUAL FEED PRIOR TO EACH FAST

The amount of the last individual feed and the hour at which it was given prior to each fast are recorded in Table 11. The first feed given to the steers following the fasts was not the same in every case. Since the interest lies, however, only in those cases where a respiration experiment was made immediately after the first refeed, the details regarding the first feed after each fast are not tabulated here, but will be discussed subsequently in connection with the respiration experiments. (See pp. 222 and 223.)

TABLE 11.—*Amounts and times of last feeds prior to fasts*

Steer	Date	Hay[1]	Meal	Time
		kg.	*kg.*	
C and D	Dec. 6, 1921	ca. 4.5	1.36	6 a. m.
C and D	Jan. 4, 1922	ca. 4.0	3.00	6 a. m.
C	Apr. 17, 1922	2.5	1.50	$6^{h}30^{m}$ a. m.
D	Apr. 17, 1922	4.4	1.50	6 30 a. m.
C	June 1, 1922	4.5	2.00	10 30 a. m.
D	June 1, 1922	2.7	2.00	7 45 a. m.
C and D	Nov. 6, 1922	Off pasture		8 a. m.
C and D	Jan. 3 to Mar. 20, 1923	4.5	1.00	8 a. m.
C	Mar. 22, 1923	3.5	1.00	8 a. m.
C and D	Nov. 4, 1923	Off pasture		3 to 4 p. m.
C, D, E, F	Feb. 12 to Apr. 8, 1924	ca. 2.5	0.00	7 to 8 a. m.
C	Apr. 22, 1924	4.5	0.00	8 a. m.
D	May 13, 1924	4.5	0.00	8 a. m.
C and D	Nov. 11, 1924	Off pasture		$4^{h}30^{m}$ p. m.
E and F	Dec. 14 and 19, 1924	3.5	0.00	8 40 a. m.
E and F	Jan. 14 to Feb. 13, 1925	3.5	0.00	5 p. m.
E and F	Mar. 1 to Apr. 22, 1925	3.5	0.00	ca. $8^{h}45^{m}$ a. m.
E and F	May 5 and 12, 1925	3.5	0.00	5 p. m.

[1] Timothy hay was fed to steers C and D on all dates and to steers E and F until March 1925. On Mar. 6, 1925, at $4^{h}30^{m}$ p. m. and thereafter steer E was fed alfalfa hay; on Mar. 9, 1925, at $4^{h}30^{m}$ p. m. and thereafter steer F was also fed alfalfa hay.

DISCUSSION OF RESULTS

BODY-WEIGHT

No one factor is of greater concern in practical and experimental nutrition than is a true measure of the loss or gain of organized body-tissue resulting from any particular level of feeding. Since there is seemingly no better measure of these changes than live body-weight, it has been almost universally adopted for this purpose. On *a priori* grounds, one can reasonably assume that in fasting, with no food intake, there must be a continuous draft upon the body-tissue. The magnitude of this draft, however, is not strictly indicated by any changes which take place in live body-weight, for even while this draft may be going on, the live weight may actually increase. In most fasting experiments, drinking-water is permitted, which of course helps to increase the live weight temporarily. On the other hand, there are factors, such as the excretion of urine and feces, which decrease the live body-weight, but which do not quantitatively represent loss of tissue. It is therefore extremely complicated to determine the true loss of body-tissue which takes place as a result of the fasting *per se*. Without a careful analysis of the relative influence of these various factors, any changes in body-weight can present only a most inadequate picture of true losses of body-tissue. The daily fluctuations in live weight due to these extraneous factors may be exceedingly large; in fact, they may be many times greater than any possible daily changes (particularly increases) which could take place in the form of body-tissue.

The gross fluctuations in the live weights of cattle from day to day, even with constant intake of food and water, have already been discussed in great detail.[a] These changes in live weight, which are at times very large, can be definitely traced in the majority of instances to variations in the fill or ballast of ruminants and particularly to variations in the water-content of the alimentary tract and of the bladder. From the experimental standpoint, it would be preferable if the caecum and the bladder could be emptied just prior to weighing at the end of any given experimental period, but obviously this is impossible in the case of ruminants. Yet if both of these organs are emptied just after the weighing at the end of the 24-hour period, these voidings may by chance be credited to either one or the other of two different days and the live weight will vary accordingly. The irregularity in the quantity and in the time of expulsion of both feces and urine is therefore an important factor in these fluctuations in live weight.

The results obtained during the undernutrition periods in this present research bear out the earlier results with ruminants published from the Nutrition Laboratory, which showed that during undernutrition there are pronounced variations in the amount of the intestinal ballast, and particularly that when there is a transition from a low to a higher nutritive plane, or vice versa, the change is relatively enormous. The variations which take place in the elimination of feces under conditions of fasting were therefore studied with special care in these fasts, the amount of each defecation and

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 80 et seq.

of each urination being recorded, as well as the hour when they were voided. Such records give no direct measure of the actual mass of undigested material in the intestinal tract at any time, but are essential to an intelligent study of those changes in body-weight which represent organized body-tissue apart from those due to changes in fill.

The body-weights of our steers were determined on scales sensitive to approximately 0.2 kg. Since the primary essential in weighing a nervous animal is quiet control, particular care was taken to have the animal standing still while the sliding weight on the scale-beam was being adjusted to a balance. The desirability of always having the animals weighed by the same person at the same hour of the day and as nearly as possible under the same conditions can hardly be over estimated. In fact, the person who held the animal also stood on the scale and was weighed with the steer, the scale having been previously balanced with the attendant's weight recorded on the upper arm of the scale beam. Thus any pull on the halter would not disturb a correct balance. The body-weights were therefore recorded with extreme care, every precaution being taken to secure the highest degree of accuracy in the measurements and in the time records, in order to make the weights of special value in the computations of the gains or losses per 24 hours and particularly in the calculation of the insensible loss.

Lengths of Fasts and Nature of Feed-levels Preceding Them

Of the 4 animals used in this investigation, steers C and D were each subjected to 7 fasts of from 5 to 14 days, one fast of 4 days, one of 3 days, and 11 and 10 fasts, respectively, of 2 days each. Steers E and F were each subjected to one fast of 5 and 6 days, respectively, to one fast of 4 days, and to 7 and 6 fasts, respectively, which were between 2 and 3 days in length. These fasts followed different levels of nutrition. All the fasts of steers C and D from December 1921 to June 1922 came after a preliminary feeding on hay and meal, the feed-level ranging from approximate maintenance to moderate supermaintenance. The fasts of November 1922 and November 1923 with the same steers took place after they had been on pasture for 4 or more months, and the fasts in March 1924 followed 2 months of submaintenance feeding. The short fasts of steers C and D, ranging from 2 to 4 days, followed feed-levels representing approximate maintenance. The long fasts of steers E and F in February 1924, like those of steers C and D in March 1924, followed submaintenance feeding, and their 4-day fasts in April 1924 followed maintenance feeding. The short 2-day and 3-day fasts of steers E and F in 1925, however, were not planned for a study of body-weight changes.

The steers were kept in metabolism stalls during all fasts and, with few exceptions, also during the preliminary feeding-periods before the fasts, so that it was possible to secure daily records of the live weight, the weights of water consumed, and the weights of urine and feces voided. The resulting mass of data has been given in detail for the fasts of steers C and D in April 1922 (see Tables 9 and 10, pp. 44 and 45), but the data for the other fasts will be found in the tables in this chapter and in the subsequent chapters of this monograph.

Daily Variations in Body-weight During Fasting

The daily variations in body-weight have been tabulated for each fast and for the 3 food days directly preceding. For the fasts of 5 or more days, which followed different feed-levels, the data are given in Table 12, and for the fasts of 2 and 3 days, following maintenance feeding, the data are given in Table 13. Reference should also be made to Tables 17 to 20 and Table 27, pages 72, 76, 78, 83, and 100, in connection with the following discussion.

Influence of Long Fasts at Different Levels of Nutrition

Considering, first, the fasts of 5 to 14 days, we see from Table 12 that on the three food days preceding each fast fluctuations in live weight from day to day appear in all instances, as would be expected, but since they include both gains and losses which are practically compensating, the tendency to variation around a uniform live weight is apparent. During fasting, the general picture of daily variations in live weight shows a clear-cut contrast to the conditions previous to fasting. The changes in live weight are equally large for the first three or four days, but with few exceptions they represent only losses. After the fourth day the losses continue, but they tend to become materially less, although they still remain somewhat irregular.

A close examination of the losses during different fasts shows the important influence which the prefasting feed-level exerts on losses in weight for the first few days. The first four long fasts of steers C and D (see Table 12) followed relatively similar feed-levels, consisting of hay and meal and ranging in quantity from maintenance to slightly supermaintenance. During all four of these fasts the losses in live weight on the first day are similar, but relatively small. The apparently wide discrepancy between the first fast and the three following is directly accounted for by differences in water intake at the beginning of the first 24-hour period. In other words, in the first fast both steers drank approximately 18 kg. of water at the beginning of the first 24-hour period without food, and before each of the other three fasts they took approximately double that amount, although there was no material difference in the total weight of urine and feces voided on these days. Excretion of this water in the urine and feces during the same 24-hour period, therefore, furnishes the remaining necessary evidence for the cause of these fluctuations in live weight.

In the fifth and sixth fasts, which followed pasture feeding (an entirely different feed-level), the relative losses during the first 24-hour period are at least five times as large as those during the first day of fasting after dry feed. In the sixth fast (i. e., in November 1923) the losses were obtained only for the last 5½ hours of the first 24-hour period, but even for this length of time the decrease in weight is approximately 11 kg., suggesting that the loss for the total 24 hours must have been immense, as was the case in the fifth fast in November 1922.

In the seventh fast with steers C and D, which followed a submaintenance feed-level of 2 months, there was practically no loss in weight during the first 17 hours. This fact suggests that when the fast began the intestinal fill must have been considerably below the amount normally present during

TABLE 12.—*Daily changes in body-weight before and during fasts of 5 to 14 days*

Steer and dates of fasts	Days before fast			Days fasting														
	3	2	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Steer C:	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*
Dec. 6 to 13, 1921 ..	− 8.2	+ 1.2	+ 6.0	−12.6	−15.0	−11.4	− 6.6	± 0.0	− 5.2	− 5.0	......	......	......	......	......	......	......
Jan. 4 to 14, 1922 ..	− 1.6	+ 3.2	+ 8.4	− 5.6	−20.4	− 6.2	− 8.8	− 6.6	− 0.8	− 8.6	− 3.4	+ 2.2	− 6.6	......	......	......	......
Apr. 17 to May 1, 1922	+ 0.4	+ 3.0	− 2.0	− 6.2	− 8.4	−12.6	− 9.6	− 4.4	− 1.8	− 8.0	− 4.4	− 4.2	− 3.0	− 4.0	− 6.2	− 4.2	− 1.8
June 1 to 7, 1922 ..	− 1.8	− 3.2	+ 5.0	− 4.4	−15.2	−16.6	− 9.4	+ 1.8	−11.8	......	......	......	......	......	......	......	......
Nov. 6 to 16, 1922 ..	......	......	......	−32.0	−18.0	− 2.8	−13.0	− 7.4	− 1.8	− 4.8	+ 0.4	− 7.8	+ 6.4	......	......	......	......
Nov. 4 to 10, 1923 ..	......	......	......	[1]−11.8	−29.8	−18.2	−10.6	− 8.8	......	......	......	......	......	......	......	......	......
Mar. 3 to 13, 1924 ..	− 4.4	+ 1.0	− 2.0	[2]− 0.4	− 6.4	− 7.6	− 6.2	− 3.6	− 5.0	− 4.4	− 3.4	− 3.2	− 4.2	......	......	......	......
Steer D:																	
Dec. 6 to 13, 1921...	+ 8.0	+ 0.4	+ 1.4	−13.4	−11.0	− 6.2	+ 0.4	− 7.0	− 6.2	+ 3.0	......	......	......	......	......	......	......
Jan. 4 to 14, 1922 ..	+ 4.4	+ 6.0	+ 3.6	+ 0.8	−18.4	− 2.4	−12.4	+ 7.4	− 8.2	+ 0.4	− 7.4	− 3.0	+ 2.4	......	......	......	......
Apr. 17 to May 1, 1922	+ 1.6	+ 3.4	− 2.0	− 4.8	−10.6	− 9.2	− 6.0	− 6.8	− 0.8	− 7.0	− 0.2	− 3.0	− 3.8	− 6.8	− 1.2	− 6.6	− 5.4
June 1 to 6, 1922 ..	− 3.0	+ 4.0	− 3.4	− 0.2	−18.2	− 7.2	−10.4	+ 2.4	......	......	......	......	......	......	......	......	......
Nov. 6 to 14, 1922 ..	......	......	......	−33.8	− 4.4	−11.4	− 9.4	+12.4	− 7.8	− 6.4	− 5.2	......	......	......	......	......	......
Nov. 4 to 9, 1923 ..	......	......	......	[1]−10.2	−37.4	−16.0	+ 5.2	− 7.4	......	......	......	......	......	......	......	......	......
Mar. 3 to 12, 1924 ..	+ 1.6	− 2.0	+ 1.2	[2]± 0.0	−12.4	− 7.8	+ 4.2	− 7.6	− 5.4	+ 3.0	− 5.8	− 3.4	......	......	......	......	......
Steer E:																	
Feb. 12 to 17, 1924...	+ 2.8	− 4.0	+ 3.0	− 5.4	− 4.4	− 3.6	− 1.0	− 2.6	......	......	......	......	......	......	......	......	......
Steer F:																	
Feb. 12 to 18, 1924...	+ 4.8	− 5.0	+ 6.2	− 9.2	− 4.8	− 5.6	− 1.4	− 1.8	+ 2.8	......	......	......	......	......	......	......	......

[1] Loss during last 5½ hours of the 24-hour period; loss during first 18½ hours not known.

[2] Loss for only 17 hours (2 p. m. to 7 a. m.) instead of the usual 24 hours, as the beginning of the 24-hour period was changed from 2 p. m. to 7 a. m. at the end of the first fasting day.

maintenance feeding. The losses noted during the submaintenance fasts of steers E and F, although not quantitatively comparable with the losses of steers C and D, because of inequality in the size and age of the animals, are surprisingly high on the first day, but the losses on the following days are small, characteristic of submaintenance feeding.

The influence of water intake on the irregularity of the loss in live weight becomes strikingly manifest between the first and the second day of fasting. In the fasts of 5 to 14 days, almost without exception the animals would refuse water at the beginning of the second day, after having fasted for 24 hours. Hence, in most instances, there was no intake whatsoever to offset the outgo, and the losses are relatively large. As further proof of this point, those instances when the animal actually did drink any material quantity of water show the exception to a large decrease in weight. Striking examples are the third fast of steer C and the fifth fast of steer D. On the other hand, in the short 2-day fasts, which will be discussed in detail later (see Table 13, p. 60), when these steers refused to drink at the beginning of the first day, but drank at the beginning of the second day, the magnitude of live-weight losses was reversed. In other words, it is purely a differential balance produced by water intake on the first and second days, which indicates a larger loss in weight on the second day than on the first, or vice versa. The relationships between loss in weight and water intake are of course not absolutely proportional, as they are modified somewhat by variations in the amount of urine and feces voided. The variations in urine and feces, however, are not by themselves of sufficient magnitude to account for a material difference in loss of weight.

The conditions pertaining to the fasts off pasture are not strictly comparable with the conditions of the fasts following dry feed just mentioned, for the reason that animals apparently lose the semi-liquid fill of grass at a much more rapid rate than they do a fill from hay and meal. The tremendous losses during the first day of these fasts off pasture have already been pointed out. During the second day of fasting off grass the loss still tends to continue at nearly the same rate when the animal does not drink water, and in the only case where the loss is very low (4.4 kg.) the cause can immediately be laid to the fact that this is the only instance where the animal drank water at the beginning of that day. In the case of the fast off pasture where the loss is exceptionally large even on the second day (37.4 kg. with steer D), the cause is immediately traceable to an exceptionally large amount of urine and feces coincident with no water intake at the beginning of the 24-hour period.

On the third day the effect of the previous feed-level becomes less manifest, and the weight loss of both steers appears to approach a relatively more stable condition. Even the maximum loss of 18.2 kg. with steer C on the third day of the fast in November 1923 is only slightly over half as large as the probable loss on the second day of the same fast. The loss shows a still further decline on the fourth day, and it is at this point that steers C and D show the greatest individual difference. For the first four days the live-weight losses of steer C were in general greater than those of steer D, and on the fourth day his average loss for the 7 fasts was more than twice that of steer D. On the other hand, steer D had consistently taken much larger amounts of water and a particularly large amount on the fourth day. After the fourth day the rate of the daily loss of both animals appears to become similar, regardless of the prefasting feed-level or of the individual animal.

The average daily loss of steers C and D from the fifth day on to the fourteenth is, respectively, 3.9 and 3.7 kg. The close agreement between these average losses after the fifth day and the insensible perspiration during the same period (see Table 17, p. 72) suggests that after the fifth day the loss in weight is more closely representative of the loss in body-tissue, i. e., muscle and fat. If the outgo of visible excreta were always proportional to the intake of food and water during the same 24-hour period, then any loss or gain in weight during this time could be accepted as a reasonably close measure of loss or gain in body-tissue. Under conditions, however, where the intake (water only) from one day to another may vary between 0 and 50 kg. and the visible outgo may remain fairly uniform, the differential between these two extraneous factors entirely conceals any change in the body-tissue. In other words, the live weights on any given day are not specifically indicative of a change in body-tissue unless due allowance is made for the balance between the intake and outgo of visible matter.

In the earlier literature there are no data with which our results may be compared, except the experiments of Grouven.[a] One of his oxen, which weighed 522 kg., fasted for 8 days. The loss in weight from day to day was, as with our animals, rather large. Considerable irregularity was noted in the loss in weight at the end of the fast, an irregularity which was, however, in most instances easily accounted for by differences in water intake or in the excretion of urine and feces. With another ox, weighing at the start 420 kg., the losses in weight were more regular than with the larger animal. Considerable differences were noted in the amount of water consumed by the smaller ox, and yet he drank water every day, whereas the larger ox refused water on three days. The volume of urine with the smaller ox remained singularly constant throughout the entire fast. The amount of feces was large on the first day, but there was a rapid drop on the second day. Since, as pointed out by Grouven in his discussion of the nature of the intestinal ballast, the previous rationing plays such a rôle in the changes in live weight during fasting, it is difficult to draw any strict comparison between the data secured with our animals and with those of Grouven.

Recently, Forbes, Fries and Kriss[b] have published the body-weights of some fasting cows, which indicate that there was in general a loss in body-weight as the fast progressed, with occasional gains, due in large part to the amount of water consumed. The maximum loss was 28.9 kg. with cow 887 III, which fasted for 9 days. Cow 874 III, which weighed 100 kg. more, lost 25.5 kg. in 9 days.

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[a] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmünde, Berlin, 1864, pp. 147 et seq. (See, also, p. 15 of this monograph.)

[b] Forbes, Fries, and Kriss, Journ. Dairy Science, 1926, 9, p. 18.

INFLUENCE OF SHORT FASTS AT A MAINTENANCE LEVEL OF NUTRITION

In view of the diversity found in the losses in weight of these animals under different conditions of fasting, i. e., after pasture, after maintenance feeding, and after submaintenance feeding, it is of importance to note what would be the actual body-loss in a series of fasts where the feeding conditions prior to fasting would be practically identical throughout the entire series. In connection with a series of short fasting experiments made primarily to study the influence of environmental temperature upon metabolism, the two animals, C and D, were fed practically a constant ration for several months, receiving 9 kg. of hay and 2 kg. of meal daily from November 20, 1922, until March 27, 1923. During this time they were subjected at different times to short 2-day fasts, and on one occasion to a 3-day fast. The data for the initial and the final body-weight, the total loss in weight, and the changes in body-weight on the three days with food before the fast and on the several days of fasting, are incorporated in Table 13.[a]

TABLE 13.—*Daily changes in body-weight on feed and during short fasts at a maintenance level of nutrition*

Steer and dates of fasts (1923)	Initial body-weight	Final body-weight	Changes in weight on days before fast			Changes in weight on fasting days		Total loss in body-weight
			3	2	1	1	2	
Steer C:	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*
Jan. 3 to 6...	689.8	658.8	− 4.0	+ 4.0	− 5.4	−24.0	[1]− 2.8	31.0
Jan. 15 17...	686.4	654.2	− 6.6	+ 4.6	− 8.2	−29.6	− 2.6	32.2
Jan. 21 23...	692.8	661.4	+12.6	+ 2.2	− 4.6	−29.0	− 2.4	31.4
Jan. 28 30...	701.2	670.6	+16.6	− 6.8	+ 1.2	−26.6	− 4.0	30.6
Feb. 5 7...	700.2	670.4	− 5.6	− 0.2	+ 3.0	−25.2	− 4.6	29.8
Feb. 11 13...	695.4	667.0	+10.2	+ 5.4	− 5.8	−25.0	− 3.4	28.4
Feb. 18 20...	696.8	667.2	− 0.4	− 2.2	+ 3.2	−25.4	− 4.2	29.6
Mar. 1 3...	700.0	670.2	− 4.0	+ 4.8	− 2.0	−26.8	− 3.0	29.8
Mar. 8 10...	702.0	673.8	+ 1.4	− 1.8	+ 1.2	−27.0	− 1.2	28.2
Mar. 15 17...	703.8	674.0	+ 1.4	− 6.0	+ 0.8	−27.0	− 2.8	29.8
Mar. 22 24...	679.0	644.2	− 1.4	− 5.4	− 6.0	−30.8	− 4.0	34.8
Steer D:								
Jan. 9 to 12...	695.0	662.6	+ 2.8	[2]−22.8	+19.2	−26.0	[1]− 2.2	32.4
Jan. 17 19...	695.0	659.4	− 0.4	− 9.4	+ 2.2	−29.2	− 6.4	35.6
Jan. 25 27...	694.4	661.2	+ 7.8	− 9.8	+ 5.4	−27.0	− 6.2	33.2
Feb. 1 3...	686.4	649.6	− 5.4	− 5.0	+ 2.8	−35.0	− 1.8	36.8
Feb. 8 10...	685.2	658.4	± 0.0	− 7.8	− 5.6	−24.8	− 2.0	26.8
Feb. 14 16...	701.8	664.6	+15.0	+ 0.8	− 3.4	−26.0	−11.2	37.2
Feb. 22 24...	701.0	663.6	− 2.4	− 5.6	+ 9.4	−27.4	−10.0	37.4
Mar. 5 7...	696.0	661.0	+ 1.4	+ 1.8	+ 1.6	−25.2	− 9.8	35.0
Mar. 13 15...	695.4	669.6	− 8.4	+ 0.8	− 5.0	−24.8	− 1.0	25.8
Mar. 20 22...	693.8	656.4	+ 0.4	− 9.4	− 3.0	−30.6	− 6.8	37.4

[1] In this experiment the steer fasted 3 days. During the third day, steers C and D each lost 4.2 kg. in body-weight.

[2] The afternoon feed was withheld on this day, as it was planned to measure the standard metabolism the next morning, but the experiment was not made.

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[a] In Table 13 the change in weight during the last 24-hour period of fasting and the live weight at the end of the fast have been corrected for the first feed after the fast, consumed usually during the last 3 hours of the 24 hours, but in two cases consumed during the last 6 hours.

The changes in body-weight before fasting show the usual fluctuations noted in Table 12, and are due probably to changes in water-content and to irregularity in the expulsion of feces. The losses in weight on the first day of fasting are remarkably uniform with both animals, explainable undoubtedly by the fact that the feed-level prior to the fasts was uniform in all instances, and also by the fact that in every instance no water was drunk at the beginning of the first fasting day. Thus, with steer C the loss in weight on the first day ranges only from 24 to 30.8 kg. In the case of steer D the loss on the first day ranges from 24.8 to 35.0 kg. In general, the uniformity of ration has resulted in a strikingly uniform body-loss on the first day, amounting on the average to 27 kg. with both steers. There are obviously no instances of plus values, and the wide discrepancies noted in Table 12 here disappear. On the second day there is a pronounced drop in the loss to a level of not far from 3 to 4 kg. in the case of steer C, but in the case of steer D the change, although pronounced, is not so regular, since the loss ranges from 1.0 kg. to as high as 11.2 kg., being on the average about 6 kg. This decrease in the loss and the difference between steers C and D on the second day may be partly explained by the fact that steer C drank water in every instance at the beginning of the second day, but steer D drank only in the case of the first five fasts and the last two fasts.

In the long fasts at different feed-levels, reported in Table 12, the losses on the second day were very irregular and much higher than in these 1923 fasts, particularly with steer C. There are three explanations for this. In the first place, the ration preceding each of the short fasts in 1923 was the same, whereas the feed-levels preceding the longer fasts varied greatly. In the second place, the second day of fasting in the short fasts began exactly 30 hours after the last feed in every case, and the amount of the last feed was always essentially the same. In the long fasts, on the contrary, the second day did not begin the same number of hours after the last feed in every case, the time varying from 22 to 32 hours after the last feed. Moreover, the last individual feed preceding these long fasts varied greatly in amount and character. Furthermore, there was greater irregularity in water intake on the second day of the longer fasts.

There was one 3-day fast with each animal in the 1923 series, in which by chance the weight-loss of both steers was actually the same on the third day, namely, 4.2 kg. This loss is lower, as a matter of fact, than any of the other values found on the third day with these animals in the longer fasts, save in the case of the November 1922 fast of steer C and the January 1922 fast of steer D.

Aside from the first fast in 1923, which was 3 days long, the animals as a rule fasted about 51½ hours, so that the total losses are comparable. In 51½ hours the total loss in weight of steer C during these short fasts averaged 30 kg, and the total loss of steer D averaged 34 kg. Again a much greater regularity was exhibited by steer C than by steer D.

Losses in Body-weight During 4-Day Fasts under Similar Conditions

The losses noted during a series of 4-day fasts in April and May 1924, when the animals remained inside the respiration chamber for three out of the four days, are recorded in Table 14. Prior to these fasts all four animals had been upon a reasonably uniform nutritive plane for from 4 to 8 weeks. They were placed in the respiration chamber after having been 24 hours without food, and were left there for 3 consecutive days. The body-weights were determined only at the beginning and end of the respiration experiments, and hence the data are available only for the total loss in weight in 3 days instead of the losses during four individual 24-hour periods, i. e., the first day's loss was not obtained.

Table 14.—*Losses in body-weight during 3 days*[1] *of fasting under similar conditions*

Steer	Dates of fasts	Body-weight in November 1923	Body-weight at beginning of fast[1]	Body-weight at end of fast	Total loss in body-weight
	1924	*kg.*	*kg.*	*kg.*	*kg.*
F	Mar. 31 to Apr. 4	291.0	295.2	271.8	−23.4
E	Apr. 8 12	266.2	280.0	260.8	−19.2
C	Apr. 22 26	723.8	669.6	620.0	−49.6
D	May 13 17	707.0	664.6	621.4	−43.2

[1] Beginning 24 hours after food.

The two young animals, E and F, were first studied. In consideration of the fact that steer F weighed essentially the same at the beginning of his fast in April 1924 as at the beginning of the experimental season, namely, November 19, 1923, and that previous to this April fast he had been on a submaintenance ration for several months and had then fasted 6 days in February, it can be seen that, judging from body-weight alone, he had reached his original condition. But meanwhile he had grown, and was nearly 5 months older. In all probability, therefore, he was still in a distinctly undernourished condition. Steer E had also passed through a period of undernutrition and a 5-day fast prior to his fast in April 1924, but since his weight at the start of the April fast was somewhat greater than that noted at the beginning of the season, one would infer that he was in a somewhat better nutritive state than steer F. The two large animals, C and D, weighed noticeably less than at the beginning of the season on November 5, 1923, when they came off pasture, having been through a prolonged period of undernutrition and a 10-day fast previous to their fasts in April and May 1924. Hence they were distinctly below par at the time of these particular experiments.

In these 4-day fasts the younger steers, E and F, lost 19.2 and 23.4 kg., respectively, and the older and larger steers, C and D, lost 49.6 and 43.2 kg., respectively. Little is to be gained by attempting to apportion these losses over the four days and compare them with the losses during the two days in the short fasting experiments, or, indeed, with the individual days in the prolonged fasting experiments. The chief point illustrated by these 4-day fasts is that under essentially uniform treatment the two animals in each pair are fairly close physiological duplicates. It is impracticable to attempt to compare the weight-losses of various animals during fasting unless experiments follow the same rationing and unless the withholding of food is made at exactly the same time, the last feed having been of the same amount. If duplicate experiments are made under these conditions, the body-weight tables indicate that a reasonably close physiological duplication may be expected with two animals of the same size and age, receiving the same character and amount of feed.

General Conclusion with Regard to Significance of Changes in Body-weight

From the analysis of the changes in body-weight, not only during the long fasts but likewise during the 2-day fasts and during the consecutive 3-day experiments inside the respiration chamber, it is clear that the changes in body-weight vary greatly with respect to the animals, the different days of fasting, and the different fasts. It has already been seen that some of the major differences are explained by differences in water intake and, to a much less degree, by differences in the output of feces or urine. In each of the first four long fasts the total loss in weight of steer D was much less than that of steer C. If one considers that the water drunk during each of these fasts offsets a theoretical further loss which would have been recorded on the scales, and if one adds the total amount of water consumed to the total loss in weight in each case, one finds that the differences between the two animals practically disappear. A careful study of the amounts of water consumed on the different fasting days, the weights of urine and feces, and particularly the insensible perspiration, makes it evident that the differences in live weights themselves are wholly without significance unless the changes in these other factors are taken into consideration. The use of live weight as an index of gain or loss in body-tissue is, therefore, clearly ruled out.

LOSS THROUGH THE LUNGS AND SKIN

As early as in the observations of Sanctorius[a] and thereafter in the observations of Bischoff[b] and of Bischoff and Voit,[c] and of Grouven,[d] varying degrees of importance were attached to the loss through the lungs and skin of an animal used for experimental research. Sanctorius especially laid great stress upon this loss, which he determined in his own case by sitting upon a chair suspended from a steelyard and noting his loss in weight from hour to hour under various conditions of bodily, mental, and digestive activity. These determinations were the basis of a large number of aphorisms published by him. When quantitative methods in studying food ingestion and the excretion of urine and feces, and particularly when Henneberg's schematic conception of the animal body began to be applied, apparently the significance of the loss through the lungs and skin was disregarded.

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[a] Sanctorius, Medicina Statica, 1614; translated by John Quincy, London, 2d ed., 1720.

[b] Bischoff, Der Harnstoff als Maass des Stoffwechsels, Giessen, 1853.

[c] Bischoff and Voit, Die Gesetze der Ernährung des Fleischfressers durch neue Untersuchungen, Leipzig and Heidelberg, 1860.

[d] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmünde, Berlin, 1864.

Since recent researches at the Nutrition Laboratory[a] on humans have indicated that there is a reasonably close correlation between insensible loss and general metabolism, a special effort was made in studying these steers to secure the data for the accurate computation of the insensible loss.

The daily changes in gross live weight of a steer, especially during fasting, have little direct quantitative significance, because, as has just been emphasized, they are profoundly affected by the amount of water consumed and the feces and urine passed. If 1 kg. of water is taken into the mouth and is subsequently excreted in the urine, it plays practically no rôle in the metabolism of the animal. Similarly, if there are 100 kg. of ballast or fill in the intestinal tract of a ruminant at the beginning of a fast and 40 or 50 kg. of this fill are excreted as feces, this again has no particular bearing upon the metabolism of the animal. The insensible loss through the lungs and skin does play a rôle in the metabolism, however, for through the lungs and skin, chiefly through the lungs, passes the carbon dioxide formed in the process of oxidation. The total weight of carbon dioxide is not wholly derived from body-tissue, for the oxygen comes from the oxygen in the air, but the carbon of the carbon dioxide does represent true body-loss. The amount of carbon excreted can be computed, provided that the total carbon-dioxide output is measured either during 24 hours inside of a respiration chamber or in several periods throughout the day representative of the entire day. The water given off from the skin doubtless existed in large part as preformed water, but in the process of oxidation, particularly of fat, water is formed in which each gram of hydrogen requires 8 grams of oxygen, which it gets from the air. Furthermore, in the oxidation of carbohydrates there is a certain amount of water of chemical constitution, namely, the hydrogen and oxygen of the molecule, which exists in the proper proportion to form water. In the insensible loss from the lungs and skin, therefore, the most important factor bearing upon the metabolism is the carbon of carbon dioxide. The water given off is not, however, without significance in connection with metabolism, for it represents a method of heat-loss, each gram of water thus vaporized from the lungs and skin requiring 0.586 calorie for its vaporization.

The insensible loss, therefore, is made up of the carbon of the fat, protein, and carbohydrate burned in the body and the organic hydrogen and oxygen preexisting in these molecules, and, in addition, it is made up of the very large and variable factor of water vaporized through the lungs and skin. An analysis of the nature of the insensible perspiration is of great physiological importance. Prior to such an analysis, however, it is advisable to know the actually measured insensible loss of these steers and to note whether it has any relationship to feed or to lack of feed, activity, and other factors which are known to affect heat-production, i. e., the vaporization of water and the production of carbon dioxide.

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[a] Benedict, Carnegie Inst. Wash. Pub. No. 203, 1915, p. 84; Benedict and Hendry, Boston Med. and Surg. Journ., 1921, **184**, pp. 217, 257, 282, 297, and 329; Benedict, Boston Med. and Surg. Journ., 1923, 188, p. 127; Benedict, Bull. Soc. Sci. d'Hygiène Alimen., 1923, **11**, p. 343; Benedict, Schweiz. med. Wochenschr., 1923, **53**, p. 1101; Benedict, The correlation between perspiratio insensibilis and total metabolism, Collection of articles dedicated to the seventy-fifth birthday of Professor I. P. Pawlow, published from the Institution of Experimental Medicine in Leningrad, 1924, p. 193; Benedict and Root, Arch. Intern. Med., 1926, **38**, p. 1.

The data for computing the insensible loss must include accurate weighings of food and water intake, feces, urine, and live body-weight. The quantity of water drunk by the animal should be recorded with particular care, since the variations in the amount of water consumed at different times are much greater than the variations in the food consumed or in the excretion of urine and feces from day to day. All of these measurements must be made in definite periods, so that the computation of the insensible loss may represent the loss during a known length of time. For this purpose the steers were kept in metabolism stalls. The routine was to weigh the animal each day at exactly the same time (i. e., representing a 24-hour period), at which time the urine bottles and feces containers were removed, and clean, previously weighed receptacles substituted. The animal was then at once allowed to drink and the amount consumed was doubly checked by noting both the loss in weight of the water container and the gain in weight of the animal. The food was always given in carefully weighed portions, usually twice during the 24-hour period, about 4 p. m. and 7 or 8 a. m. Under these conditions all the data are at hand for computing exactly the insensible loss during a 24-hour period. Thus, to the initial weight of an animal on a given date at 2 p. m. is added the weight of food and water consumed during the ensuing 24 hours. To the weight of the animal at the end of the 24 hours is added the weight of feces and urine passed during the 24 hours. This sum is subtracted from the sum of the initial body-weight, water, and food, and the difference represents the insensible loss.

In computing this loss the exact times when food and water are consumed and feces and urine are excreted must be known. Only too frequently experimental data are recorded in such a manner that it is impossible to subdivide the weights of urine, feces, and food, and credit them to the proper 24-hour periods, and although all the weights may represent 24-hour periods, they do not invariably represent the same 24 hours. In our earlier report on undernutrition in steers[a] we found to our chagrin that in many instances our own data did not fulfill the above specifications, and, profiting by this experience, we attempted to have the data in this report uncontaminated by such errors. Even with all the precautions just mentioned, however, gross errors are occasionally found that are extremely annoying. It is hoped in the future to have every weighing doubly checked, and thus rule out, if possible, any errors of this type. An inherent difficulty in studying the insensible loss of these large animals is the weighing of the animal itself. To determine the live weight of an animal weighing 700 kg. to within 0.1 per cent is very difficult. The scales (see p. 55 for description) were reasonably accurate, but it required all the skill of the technician to secure accurate weights. It is seriously to be questioned whether it is right to report the live weights any more closely than to within the nearest half kilogram. Obviously, the weights of water, feed, feces, and urine can be obtained to within 10 grams.

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 85.

INSENSIBLE PERSPIRATION DURING FOOD PERIODS AND DURING 24 HOURS WITHOUT FOOD

Inasmuch as a study of the insensible loss of large ruminants has not been presented, so far as we are aware, since the days of Grouven, it seems justifiable to discuss, first, some of the data regarding the insensible loss of our steers when on feed before considering the losses during fasting. Frequently during the 4 years' study of these animals the so-called "standard metabolism," 24 hours after the last feed, was determined with the respiration chamber. In Table 15 are recorded the insensible losses of steers C, D, E, and F for those days when the standard metabolism was measured. In addition, the losses are given for the three days prior to these standard metabolism experiments, when the steers were receiving food daily at a nutritive level which had prevailed for some time. The loss on the day of the standard metabolism measurement in every case represents the loss during the first 24 hours without food, although in most instances the animal was fed just before the end of the 24 hours.

The variability in the insensible loss at the times of the different experiments is very pronounced. In the case of steer C, the values for the insensible loss noted 3 days before the standard metabolism experiments range from 3.8 to 15.6 kg. Similar ranges in the losses occur 2 days and one day prior to the experiments. On the days of the standard metabolism experiments, when the animal had usually been without food for the entire 24 hours, the range is somewhat smaller, i. e., from 2.2 to 12.8 kg., and the deviation from an average value is obviously somewhat lessened, due probably in large part to the entire lack of food. With steer D wider differences are noted, the loss ranging from 4.4 to 14.4 kg., 3 days before the metabolism experiment, from 4.2 to 18.4 kg., 2 days before, from 4.6 to 18.4 kg. on the day before, and from 3.6 to 17.6 kg. on the day of the experiment itself. With the smaller steers, E and F, the variability is naturally much less, the widest range during the food days in the case of steer E being only from 2.6 to 9.4 kg., while on the day of the standard metabolism experiment the range is only from 2.4 to 7.0 kg. With steer F the picture is essentially the same.

The general picture of the range in daily losses is that there are gross differences in the insensible loss at different times of the year. A closer examination of the data in Table 15, however, shows that on any three successive days under the same feeding conditions the loss remains reasonably uniform, and that on the days of standard metabolism experiments, when food is withheld, the loss usually decreases noticeably.

The large differences in the insensible perspiration noted in Table 15 are in large part explained by the differences in the feed-level. When steers C and D were on a realimentation or a maintenance feed-level, the insensible perspiration was almost invariably considerably higher than when they were on a submaintenance feed-level. For example, in the case of steer C the return to maintenance feeding on June 18, 1923, immediately resulted in a marked increase in the insensible perspiration. This same picture is likewise noted with steer D. It is not clear, however, that the insensible perspiration is absolutely uniform from day to day even upon the same

Table 15.—*Daily insensible loss during 3 days with food, followed by 1 day without food*[1]

Steer and date of standard metabolism experiment	Food-level[2]	Days (on food) before standard metabolism experiment						Day of experiment[3]	
		3		2		1			
Steer C:		*kg.*	°*C.*	*kg.*	°*C.*	*kg.*	°*C.*	*kg.*	°*C.*
Dec. 17, 1921	R	3.8	18	3.2	5	3.8	15	4.8	21
Dec. 22, 1921	R	4.6	12	5.0	20	8.0	13	2.2	7
Jan. 23, 1922	R	9.4	14	10.4	19	12.4	18	6.4	12
Mar. 31, 1922	M	9.6	18	9.0	17	11.0	19	7.4	20
May 9, 1922	R	7.4	19	8.0	19	8.0	18	5.2	18
Dec. 13, 1922	M	11.5	24	13.8	20	14.4	23	9.0	18
Dec. 18, 1922	M	15.6	27	14.6	24	16.0	26	12.8	26
Dec. 21, 1922	M	12.8	26	14.2	23	13.4	24	9.4	22
Dec. 26, 1922	M	13.8	21	16.6	27	12.8	20	11.2	26
Dec. 29, 1922	M	11.2	26	15.2	28	11.4	22	6.6	15
Apr. 3, 1923	M	9.0	12	9.4	10	8.4	13	9.6	21
Apr. 11, 1923	M	11.2	17	7.8	12	10.8	16	6.4	14
Apr. 18, 1923	M	9.4	13	10.2	15	10.4	15	8.2	18
Apr. 24, 1923	M	15.2	24	14.8	24	9.6	14	6.0	12
May 5, 1923	S	6.8	18	5.6	18	7.6	21	7.2	22
May 11, 1923	S	6.6	20	7.2	20	6.4	16	4.4	16
May 18, 1923	S	5.8	19	5.8	19	8.8	24	5.2	18
May 24, 1923	S	5.4	21	5.2	18	5.8	17	4.4	17
June 18, 1923	M	11.4	20	9.6	18	12.8	20	7.4	20
Steer D:									
Dec. 17, 1921	R	4.4	18	4.2	5	4.6	17	6.8	21
Dec. 22, 1921	R	6.4	12	6.0	20	7.8	13	3.6	7
Jan. 23, 1922	R	8.2	14	10.8	19	11.0	18	6.2	12
Mar. 31, 1922	M	9.2	18	8.6	17	9.8	19	6.8	20
May 9, 1922	R	5.8	19	7.2	19	6.6	18	5.6	18
Dec. 15, 1922	M	14.4	23	12.0	18	16.0	24	13.0	27
Dec. 19, 1922	M	12.6	24	15.6	26	16.6	26	11.8	23
Dec. 22, 1922	M	11.8	23	11.4	24	12.8	22	9.6	22
Dec. 30, 1922	M	12.6	28	10.8	22	8.8	15	17.6	13
Jan. 3, 1923	M	7.2	11	12.8	15	9.8	12	6.2	11
Apr. 4, 1923	M	8.8	10	9.4	13	14.6	21	6.6	18
Apr. 12, 1923	M	7.6	12	13.8	16	7.6	14	7.8	14
Apr. 19, 1923	M	9.2	15	8.4	15	9.2	18	6.4	14
Apr. 25, 1923	M	13.2	24	9.8	14	6.8	12	9.0	20
May 4, 1923	S	6.6	....	6.0	18	5.8	18	5.8	21
May 12, 1923	S	7.6	20	5.6	16	5.4	16	8.2	24
May 19, 1923	S	4.8	19	8.2	24	4.8	18	5.6	21
May 25, 1923	S	5.4	18	7.4	17	5.4	17	6.2	22
June 1, 1923	S	6.2	20	6.2	18	5.6	19	7.2	19
June 8, 1923	S	11.8	28	11.0	27	7.0	22	4.2	18
June 16, 1923	M	8.0	16	7.6	18	9.0	20	9.4	18
June 22, 1923	M	14.0	27	18.4	30	18.4	30	12.2	26
Steer E:									
Nov. 26, 1923	M	7.2	13	6.8	21	8.6	23	6.4	16
Dec. 3, 1923	M	7.8	15	8.0	14	7.4	12	5.8	15
Dec. 10, 1923	M	8.0	16	6.4	13	9.4	18	6.6	20
Dec. 17, 1923	M	8.8	15	6.8	13	6.0	14	7.0	14
Dec. 28, 1923	S	3.0	10	2.6	13	3.8	15	4.6	15
Dec. 31, 1923	S	4.6	15	4.2	16	3.0	13	3.2	14
Jan. 8, 1924	S	2.4	11	3.8	15	......	....	2.4	15
Jan. 14, 1924	S	......	....	3.2	12	3.2	14	2.6	....
Jan. 21, 1924	S	......	....	3.4	14	3.0	18	3.6	11
Jan. 28, 1924	S	3.0	16	3.4	10	2.6	10	3.0	11
Feb. 4, 1924	S	3.2	13	4.0	15	2.8	13	2.4	15

TABLE 15.—*Daily insensible loss during 3 days with food, followed by 1 day without food*[1]—Con.

Steer and date of standard metabolism experiment	Food-level[2]	Days (on food) before standard metabolism experiment						Day of experiment[3]	
		3		2		1			
		kg.	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Steer F:									
Nov. 27, 1923	M	8.0	21	7.8	23	7.6	16	5.4	18
Dec. 4, 1923	M	7.0	14	5.8	12	7.0	15	5.4	16
Dec. 11, 1923	M	3.6	13	8.6	18	......	....	8.0	18
Dec. 18, 1923	M	6.6	13	7.0	14	7.2	14	4.0	10
Dec. 29, 1923	S	2.4	13	3.4	15	4.2	15	3.4	16
Jan. 2, 1924	S	3.2	13	3.2	14	4.0	15	3.2	12
Jan. 9, 1924	S	3.4	15	3.0	15	3.2	15	2.8	16
Jan. 17, 1924	S	2.6	..	3.0	15	2.8	16	3.4	18
Jan. 22, 1924	S	2.6	14	3.6	18	2.4	11	2.6	13
Jan. 29, 1924	S	1.8	10	2.4	10	......	....	3.2	18
Feb. 5, 1924	S	2.4	15	2.8	13	3.2	15	3.0	17

[1] The temperature figure at the right of each insensible perspiration figure represents the stall temperature during the same 24 hours in which the insensible perspiration was measured.

[2] R, realimentation after fast (steers C and D, 4 to 8 kg. hay); M, maintenance level (steers C and D, 9 kg. hay and 2 kg. meal, Dec. 13, 1922, to Jan. 3, 1923, and 9 kg. hay, Mar. 31, 1922, Apr. 3–25, 1923, and June, 1923; steers E and F, 5 kg. hay and 0.68 kg. meal); S, submaintenance level (steers C and D, 4.5 kg. hay; steers E and F, 2.5 kg. hay and 0.30 kg. meal).

[3] During the 24 hours represented by the insensible perspiration recorded for the day of the experiment either no food at all was eaten or no food was eaten until near the end of the 24 hours.

ration, for relatively wide differences do still exist. But in general, with the submaintenance ration the insensible loss is low and with the maintenance ration it is high. The situation is exactly duplicated in the case of steers E and F, but since their body-weights are much smaller, the insensible perspiration is naturally smaller than that of steers C and D. Even with these two smaller animals, however, it can be seen that on submaintenance rations the insensible perspiration is perceptibly lower than on maintenance rations. Thus, the data show clearly a relationship between the feed-level and the insensible perspiration. Since it is known that with the higher feed-level there is a higher metabolism, this relationship between the feed-level and the insensible loss is the first clue that there is a relationship between the insensible perspiration and the metabolic level. This latter relationship has been most carefully studied with humans and has been shown to exist with remarkable accuracy, indeed, so much so that it has been proposed to predict the metabolism of humans from the insensible perspiration carefully determined under standard conditions.[a]

In Table 15 the individual figures for the separate days have been given and no attempt has been made to smooth out the irregularities, but it is clear that with ruminants the feed-level is not the sole factor in determining the intensity of the insensible perspiration. Indeed, we noted early in the research that the environmental temperature played a not insignificant rôle. Thus, the variations in the insensible loss occasionally noted even on consecutive days, i. e., with a constant feed-level, can be fairly closely corre-

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[a] Benedict and Root, Arch. Intern. Med., 1926, 38, p. 1.

lated, in most instances, with large differences in the environmental temperature. Since the insensible loss is made up in large part of vaporized water, it is not surprising that changes in environmental temperature affect the insensible loss, because of their effect upon the vaporization of water both from the lungs and skin. A full understanding of the data in Table 15 can therefore only be had by taking into consideration the stall temperatures under which the determinations of the insensible perspiration were made. The stall temperatures, expressed in degrees centigrade, have accordingly been incorporated in the table.

A comparison of the insensible losses and environmental temperatures on consecutive days, i. e., with constant feed-level, indicates that generally the high temperature is accompanied by a relatively high insensible loss. There are, however, exceptions to this with sufficient frequency to make it difficult to draw more than a general conclusion. Thus, in the experiment of December 22, 1921, steer C had an insensible perspiration of 4.6 kg. 3 days before the metabolism test, 5.0 kg. 2 days before, and 8 kg. on the day before, with stall temperatures of 12°, 20°, and 13° C., respectively. On the day of the standard metabolism experiment the loss was but 2.2 kg., with a temperature of 7° C. The differences in temperature and the fairly even insensible perspiration in these first experiments with steer C can be discussed only with considerable caution. Since the first two experiments with steer C were made during the realimentation period following a 7-day fast, it is not inconceivable that the insensible perspiration may have reached a minimum level due to the previous fasting, below which it could not drop appreciably even with a marked fall in temperature. Hence the low values of 3.2 kg. on the second day before the experiment on December 17, with a temperature of 5° C., and of 3.8 kg. on the next day, with a rise in temperature of 10° C., may be explained by the fact that the animal had already reached a very low level as a result of the 7-day fast.

The general picture, however, is that with high environmental temperatures and a constant feed-level there appears frequently a large insensible loss, which might be caused by an increased vaporization of water from the lungs and skin as a result of the high temperature. Obviously, wind velocity and humidity should also be taken into consideration. When in the metabolism stalls, the animals were not exposed to drafts and presumably on each day the movement of air was essentially the same, for the laboratory was well constructed, so that there was a minimum amount of draft. Inside the respiration chamber the air was invariably moved, but not violently, by an electric fan, to insure equalization in its chemical composition. The steers were therefore not subjected to excessive movement of air during the metabolism experiments.

From this analysis of the data in Table 15, the conclusion can be drawn that *the insensible loss from day to day, under the same conditions of feeding, and particularly if the environmental temperature is constant, is reasonably uniform.* Indeed, this conclusion is substantiated by Grouven's study of the insensible loss, which he computed to be astonishingly constant from day to day with animals under uniform conditions of feed and temperature. The withholding of food, on the day of the standard metabolism experiment, results usually in a pronounced fall in the daily insensible loss, provided that the temperature conditions remain uniform. Since the metabolism is known to be lowered as the result of the absence of digestive activity, it would appear as if, in this respect at least, the insensible loss were correlated with the total heat-production.

INSENSIBLE LOSS DURING THREE DAYS WITH FOOD, FOLLOWED BY TWO AND THREE DAYS WITHOUT FOOD, AT A MAINTENANCE LEVEL OF NUTRITION

In connection with another series of respiration experiments carried out on steers C and D during short periods of fasting at a maintenance feed-level, records of the insensible loss are available for the three days with food prior to the fast and for each of the two or three days of fasting. These records are given in Table 16, in which the first day of fasting corresponds exactly with the day of the standard metabolism experiment recorded in Table 15, except that the steers were given no feed at all during this first day, while on the day of the standard metabolism experiment they were in most cases fed just before the end of the day. But obviously in this latter

TABLE 16.—*Daily insensible loss during 3 days with food, followed by 2 days without food*

Steer and dates of fasts (1923)	Days before fast (with food)						Days fasting[1]			
	3		2		1		1		2	
Steer C:	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Jan 3 to 6[2]	12.6	15	9.8	12	9.0	11	6.2	6	3.0	9
Jan. 15 17	15.2	25	13.4	20	15.6	26	11.8	29	3.0	12
Jan. 21 23	13.6	28	18.6	27	18.0	29	10.8	28	4.4	7
Jan. 28 30	8.8	11	16.8	26	9.4	11	4.8	8	5.0	25
Feb. 5 7	9.8	12	8.2	4	7.8	7	5.2	6	2.8	5
Feb. 11 13	8.2	8	10.2	10	9.2	11	4.6	8	2.8	8
Feb. 18 20	7.4	−3	7.2	3	8.0	7	3.4	4	3.6	0
Mar. 1 3	9.2	12	10.8	13	9.4	11	6.2	12	3.6	14
Mar. 8 10	6.6	4	8.0	3	7.0	4	4.6	4	3.0	6
Mar. 15 17	11.2	9	10.4	7	9.8	5	5.2	8	3.8	8
Mar. 22 24	15.2	19	18.8	24	[3]20.2	27	14.8	26	8.8	22
Steer D:										
Jan. 9 to 12[2]	8.2	8	[4]5.6	11	8.2	12	6.4	13	3.4	9
Jan. 17 19	16.4	26	17.8	29	11.2	12	6.0	12	8.2	28
Jan. 25 27	9.2	7	10.6	13	8.6	11	5.8	11	6.8	26
Feb. 1 3	16.0	25	18.2	28	16.8	23	12.6	23	3.4	12
Feb. 8 10	7.6	6	5.6	5	8.0	7	5.0	8	3.2	10
Feb. 14 16	6.8	8	8.2	8	6.8	6	4.6	−3	2.4	−3
Feb. 22 24	7.6	0	6.4	6	7.6	6	4.4	2	3.2	−2
Mar. 5 7	10.0	14	9.0	11	7.4	5	3.8	4	3.8	3
Mar. 13 15	8.2	5	8.8	7	10.2	9	6.0	7	3.8	5
Mar. 20 22	10.0	7	19.4	24	15.6	19	14.2	24	10.4	27

[1] The first day begins at 2 p. m., the last feed being given between 7 and 8 a. m. The loss during the last day of fasting may be influenced by the first feed following the fast, given usually during the last 3 hours of the day (in two cases given during the last 6 hours).

[2] On Jan. 6 and 12 steers C and D fasted a third day, and the insensible perspiration was 2.8 and 3.0 kg., respectively.

[3] High value possibly due to rise in temperature and limitation of water consumption. After Mar. 15 the steers were limited to 27 kg. of water daily.

[4] Food withheld for respiration experiment, but experiment not made.

instance the weight of feed was taken into consideration in computing the insensible perspiration.

From the data for the three days with food prior to the fast, essentially the same conclusion may be drawn as was drawn from the data in Table 15, namely, that under uniform conditions of feeding and environmental temperature the insensible loss on three successive days is reasonably constant. When there is a marked rise in temperature, the insensible loss is usually somewhat increased. On the first day of fasting, in contradistinction to the results on the days of standard metabolism experiments, there is invariably a decrease, at times very pronounced. On the second day there is usually a still greater decrease. The loss on the first day of fasting ranges in the case of steer C from 3.4 to 14.8 kg. and in the case of steer D from 3.8 to 14.2 kg. This variability in large part disappears on the second day, the range being only from 2.8 to 8.8 kg. with steer C and from 2.4 to 10.4 kg. with steer D. The influence of environmental temperature is well marked. Thus, on the second day of fasting the two greatest losses with steer C (5 and 8.8 kg.) are coincidental with the two highest temperatures (25° and 22° C.), and with steer D the highest temperatures (28° and 27° C.) occur simultaneously with the two highest losses (8.2 and 10.4 kg.). In the one experiment when the steers fasted for 3 days the loss on the third day is essentially that on the second day, namely, about 3 kg. with each animal.

In Table 16, due in large part to the fact that the feed-level was in all cases constant, the evidence is much more striking than in Table 15—that there is a regular loss from day to day with uniform conditions of feed and environmental temperature. During fasting there is invariably a pronounced decrease in the insensible perspiration on the first day and a much greater decrease on the second day. The loss of both animals is remarkably uniform throughout the entire series on the second day, except in the last experiment with each steer, when a high insensible loss, probably due to the high environmental temperature, was noted.

Insensible Loss During Five to Fourteen Days without Food

Having noted the reasonable regularity in the insensible loss on succeeding days of uniform feed and environmental temperature, the pronounced decrease in loss on the first day of fasting, and the still further pronounced decrease on the second day to a reasonably uniform loss in the case of both animals of about 3 or 4 kg. per day, we may pass to an examination of the insensible loss during longer periods of fasting, as recorded in Table 17.

In these longer fasting experiments unusual precautions were taken to secure the greatest accuracy in all records of weights, additional student labor being employed to check the weights. Even with these precautions, the record for steer C on the day before the fast in December 1921 has had to be discarded because of an obvious error in recording one of the weights.

On the three successive days prior to each fast there is a reasonable degree of uniformity in the loss, although the level of the loss varies greatly in the different experiments. Thus, the average loss of steer C for 3 days prior to the March 1924 fast was 6.9 kg., but the average amount prior to the other fasts was approximately twice this amount. The same picture is shown in the losses of steer D during the three days before the fasts. The

TABLE 17.—*Daily insensible perspiration during 3 days with food, followed by 5 to 14 days without food*

Steer and dates of fasts	Days before fast (with food)						Days fasting					
	3		2		1		1		2		3	
	kg.	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Steer C:												
Dec. 6 to 13, 1921	10.0	9	10.0	7	....	....	4.0	5	3.4	5	1.6	15
Jan. 4 14, 1922	16.0	16	13.8	16	12.0	14	11.6	20	7.0	20	4.8	20
Apr. 17 May 1, 1922	17.2	21	15.4	17	16.6	20	12.6	20	6.0	20	7.2	20
June 1 7, 1922	18.4	24	16.6	22	16.8	23	10.8	23	5.2	22	5.6	23
Nov. 6 16, 1922	....	....	....	....	....	....	12.6	....	7.8	....	8.0	....
Nov. 4 10, 1923[1]	....	....	....	....	....	....	....	....	6.2	....	3.8	....
Mar. 3 13, 1924	7.4	13	6.6	16	6.8	17	[2]2.8	14	1.4	16	2.6	16
Steer D:												
Dec. 6 to 13, 1921	10.0	9	9.0	7	9.2	7	4.4	5	3.2	5	3.2	15
Jan. 4 14, 1922	17.0	16	15.0	16	16.2	14	11.4	20	7.0	20	5.0	20
Apr. 17 May 1, 1922	15.0	21	13.2	17	15.8	20	12.4	20	4.2	20	5.2	20
June 1 6, 1922	16.6	24	14.2	22	15.8	23	9.2	23	6.2	22	6.2	23
Nov. 6 14, 1922	....	....	....	....	....	....	14.0	....	9.4	....	8.8	....
Nov. 4 9, 1923[1]	....	....	....	....	....	....	....	....	11.6	....	5.0	....
Mar. 3 12, 1924	5.6	13	7.4	16	6.2	17	[2]3.0	14	3.4	16	2.8	16
Steer E:												
Feb. 12 to 17, 1924	3.2	12	2.4	12	3.4	13	3.2	16	1.8	15	2.2	16
Steer F:												
Feb. 12 to 18, 1924	2.8	12	3.0	12	2.0	13	3.6	16	1.2	15	2.2	16

Steer and dates of fasts	Days fasting											
	4		5		6		7		8		9	
	kg.	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Steer C:												
Dec. 6 to 13, 1921	3.2	20	2.8	18	2.2	17	2.2	20	....	....	....	....
Jan. 4 14, 1922	5.4	21	3.6	24	4.2	20	4.0	20	3.6	.21	3.6	23
Apr. 17 May 1, 1922	2.4	15	3.2	20	4.2	22	3.8	22	3.6	22	4.0	23
June 1 7, 1922	4.6	25	5.0	27	....	....	....	....	....	....	....	....
Nov. 6 16, 1922	7.2	....	3.0	....	1.6	....	2.4	....	2.0	....	4.0	....
Nov. 4 10, 1923[1]	3.0	....	2.8	....	....	....	....	....	....	....	....	....
Mar. 3 13, 1924	1.8	16	1.4	14	3.8	16	1.6	18	1.0	14	2.4	16
Steer D:												
Dec. 6 to 13, 1921	3.8	20	3.6	18	2.4	17	3.2	20	....	....	....	....
Jan. 4 14, 1922	6.8	21	5.2	24	4.0	20	3.0	20	4.0	21	4.4	23
Apr. 17 May 1, 1922	4.2	15	3.0	20	3.8	22	3.6	22	3.8	22	4.6	23
June 1 6, 1922	5.2	25	....	....	....	....	....	....	....	....	....	....
Nov. 6 14, 1922	8.6	....	3.6	....	3.0	....	2.6	....	....	....	....	....
Nov. 4 9, 1923[1]	4.8	....	4.0	....	....	....	....	....	....	....	....	....
Mar. 3 12, 1924	2.8	16	2.2	14	2.8	16	4.0	18	2.2	14	1.4	16
Steer E:												
Feb. 12 to 17, 1924	2.6	15	....	....	....	....	....	....	....	....	....	....
Steer F:												
Feb. 12 to 18, 1924	1.8	15	2.2	14	....	....	....	....	....	....	....	....

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[1] Stall temperature, Nov. 5, 1923, ca. 20° C.; Nov. 6, 19° C. in daytime, 15° C. at night; Nov. 8, from ca. 20° C. to 12° or 13° C.; daily records not kept of stall temperature until Nov. 23, 1923.

[2] This value represents a period of only 17 hours, from 2 p. m. to 7 a. m.

Table 17.—*Daily insensible perspiration during 3 days with food, followed by 5 to 14 days without food*—Continued

Steer and dates of fasts	Days fasting									
	10		11		12		13		14	
Steer C:	*kg.*	*° C.*	*kg.*	*° C.*	*kg.*	*° C.*	*kg.*	*° C.*	*kg.*	*° C.*
Jan. 4 to 14, 1922	4.2	23	....	....	....	....	....	....	....	....
Apr. 17 May 1, 1922	4.8	20	2.0	22	3.0	21	3.6	21	3.4	21
Mar. 3 13, 1924	2.0	16	....	....	....	....	....	....	....	....
Steer D:										
Jan. 4 14, 1922	4.0	23	....	....	....	....	....	....	....	....
Apr. 17 May 1, 1922	3.4	20	3.2	22	2.8	21	4.2	21	2.8	21

striking difference between the loss prior to the fast in March 1924 and the losses prior to the earlier fasts is explained by the fact that in March 1924 both animals were upon a submaintenance ration and were very much undernourished. They had lost in live weight, to be sure, but not in proportion to the decrease in insensible loss. The losses on the days with high temperatures are, in general, as noted earlier, somewhat higher than on the days with low temperatures. Thus, with steer C, the minimum losses, aside from those in March 1924, occur with temperatures of 7° and 9° C., and the maximum losses are coincidental with temperatures of 22° to 24° C. The minimum losses of steer D are also coincidental with the low temperatures of 7° and 9° C., but the correlation between the high temperatures and the maximum losses is not so pronounced as with steer C. The low values found in March 1924 with both animals may not be ascribed to a low environmental temperature, for the temperatures are not far from those in January and April 1922, when twice as great an insensible loss was noted with both animals. Thus the clear effect of submaintenance feeding is seen.

The smaller animals, E and F, were placed upon a submaintenance ration prior to their long fasts. In their case there is considerable uniformity in the loss from day to day prior to the fast, the values for the two steers showing close agreement. The influence of temperature plays no rôle here, for essentially the same temperature was noted each day.

In the fasting experiments proper there is in all instances a striking drop in the loss of the two large steers on the first day of the fast, but practically no change in the loss of the two small animals. The large decrease noted in the fasts of steers C and D following the submaintenance feeding, however, is partly explained by the fact that the first day of this fast was only 17 hours long, instead of the usual 24 hours. The losses of steers C and D on the first day of fasting again show a reasonably close correlation with the environmental temperature, since the lowest losses (with the exception of the losses in the March 1924 fasts) occur at the lowest temperature (5° C.). On the second day of fasting there is a still further drop in the case of all animals, a drop which amounts on the average to somewhat less than 50 per cent of the loss on the first day. On the third day a further drop is noticed in 7 instances, but on the average the loss is not materially different on the third day. After the third day, and more especially after the fourth day, there is a general tendency for the losses to be not far from 3 to 4 kg., although occasionally values as low as 2 kg. and under are noted.

The uniformly low insensible loss from the second day of fasting to the end of the fast in the case of both steers C and D in the fast following submaintenance feeding in March 1924 is striking. An average figure of 2.5 kg. per day could be assumed to represent their daily insensible loss during this fast.

A striking correlation between environmental temperature and insensible loss, after the first few days of fasting, is not apparent, although there are instances when low values appear with low temperatures and higher values with the higher temperatures.

The variability in environmental temperature complicates the interpretation of the effect of different nutritive levels, but nevertheless the evidence is sufficient to conclude that the most potent factor in determining the magnitude of the insensible perspiration is the general nutritive plane or metabolic level. In other words, the insensible loss probably is closely correlated with the total 24-hour metabolism of the animal at the time the insensible loss is measured. To prove this conclusion, however, 24-hour metabolism experiments should be made simultaneously with the measurements of insensible perspiration. Such simultaneous measurements were unfortunately not made. In the 3-day metabolism experiments which were made, it was possible to determine the insensible perspiration only on the 3-day basis, and the difficulties of collecting urine and feces in a chamber at that time not specially provided with feces ducts were such as to preclude accurate measurements of weights of feces for such computation. It is believed, however, that the evidence is sufficiently striking to make it incumbent upon all workers who are studying large animals in respiration chambers permitting 24-hour experimental periods to lay special emphasis upon collecting the data for computing the insensible loss. Changes in body-weight from day to day during fasting are only a very crude index of the change in body substance. The insensible loss, on the other hand, is more closely correlated with the nutritive plane and, in all probability, when carefully measured, bears a close relationship to the actual loss of tissue through metabolism.

It is not mere coincidence that the daily insensible loss of these steers was largest when they were on heavy rations. Thus, our detailed data show that when steer C was receiving an average daily ration of 8 kg. of hay and 1.36 kg. of meal, his insensible perspiration was on the average 9 kg. During fasting this fell to an average of about 2.5 kg. Subsequently, when he was given 7 kg. of hay and 6 kg. of meal, his insensible perspiration increased to 16 kg. on the average. Even in the case of the small animals, E and F, when they were receiving an average ration of 5 kg. of hay and 0.7 kg. of meal, the daily insensible loss ranged not far from 7 to 8 kg. When the ration was reduced to one-half, the loss immediately fell to not far from 3.5 kg. During the actual fasting experiments this loss fell still further, and with the resumption of feeding increased.

The evidence, therefore, although admittedly complicated by the factor of environmental temperature, strongly suggests a close correlation between the insensible loss of these large ruminants and their nutritive plane or 24-hour metabolism. It is believed that this correlation is sufficiently close to justify making records of the insensible loss as a part of the regular routine in all careful metabolism studies. Indeed, it is believed that the prediction of the total daily metabolism of steers may actually be made with close approximation if the insensible loss, under controlled conditions of temperature, is accurately known. The same correlation between the insensible loss and the metabolic activity of humans has been frequently noticed at the Nutrition Laboratory, and its experiments on this point have recently been reported.[a]

A series of measurements of the insensible loss, made on animals at varying nutritive planes, but at a uniform temperature to rule out the disturbing factor of environmental temperature, is most essential. Apparently with ruminants the effect of environmental temperature upon the insensible loss may be much greater than with humans. With humans the insensible loss may be considered as coming from two sources, from the lungs and from the skin. The loss from the skin is seemingly unaffected by ordinary changes of temperature (up to 25° C.), wind velocity, and air movement. The loss from the lungs is in large part determined by the carbon-dioxide production in the body, i. e., the metabolism. Indeed, so closely has this relationship been established with humans that the measurement of the insensible perspiration has been used as an index of the total metabolism. Undoubtedly any factor affecting total metabolism, such as activity and particularly the nutritive plane, and possibly the environmental temperature, will alter the insensible loss.

DRINKING-WATER

When animals are completely deprived of food and water, the processes of metabolism in which katabolism predominates can be studied in their simplest terms. With the current belief that water plays an insignificant rôle in metabolism, it seems at first sight immaterial whether water is withheld or not. Some species of animals, namely, the carnivora, and particularly the dog, can live for an incredibly long time without water and food. Thus, Awrorow's dogs withstood fasting, without water, for 44 or more days.[b] But the fasting metabolism of the dog involves the disintegration of protein and muscle to such a large extent that sufficient water is released for physiological purposes. Experience with other animals, however, has shown that the withdrawal of water hastens the approach of severe distress and finally death. For experimental purposes in the laboratory, therefore, usually food alone is withheld. Indeed, in all the fasting experiments made by the Nutrition Laboratory or by its cooperative investigators, this procedure has been followed. Thus, the man who fasted for 31 days received

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[a] Benedict and Root, Arch. Intern. Med., 1926, 38, p. 1.

[b] Awrorow, Metabolism and energy production of the organism during complete fasting. Dissertation, St. Petersburg, 1900. (In Russian.)

from 750 to 900 c. c. of distilled water per day,[a] and geese which fasted for 30 days or more were invariably allowed to drink water as desired.

The consumption of large amounts of water by ruminants, especially when they are fed in the barn, is a natural consequence of their eating large amounts of highly desiccated feed, such as hay and grain. When animals are on pasture, the succulent grass furnishes of itself a large amount of water, but even this source of supply is usually supplemented by drafts of water from time to time. The consumption of water has commonly been considered as being determined to great extent by the amount of food eaten. Kellner[b] assumes that for each kilogram of dry matter in feed about 4 kg. of water will be needed when animals are on full ration. In the study of undernutrition in steers it was found that more nearly 2.5 or 3 kg. of water were consumed per kilogram of dry matter in feed, when the animals were on a submaintenance ration consisting exclusively of hay.[c] When no food is given to these large ruminants, it is not impossible to conceive that no water would be necessary and that, since the disintegration of flesh would give enough water to carry off the waste products, the animals would act much like dogs, which withstand the complete withdrawal of food and water

TABLE 18.—*Daily water consumption prior to and during 2-day fasts, steers C and D*[1]

Steer and dates of fasts (1923)	Days before fast			Days fasting		
	3	2	1	1	2	3
Steer C:	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*
Jan. 3 to 6	25.4	28.6	18.2	0.0	9.8	6.2
Jan. 15 17	24.4	36.0	22.6	0.0	9.4	....
Jan. 21 23	37.4	33.4	29.8	0.0	10.4	....
Jan. 28 30	37.0	26.6	28.2	0.0	9.4	....
Feb. 5 7	21.6	27.0	25.8	0.0	9.0	....
Feb. 11 13	30.4	26.8	18.6	0.0	10.6	....
Feb. 18 20	18.4	21.6	27.6	0.0	9.6	....
Mar. 1 3	20.6	30.0	23.8	0.0	10.4	....
Mar. 8 10	21.4	23.2	23.8	0.0	10.0	....
Mar. 15 17	28.0	22.2	26.6	0.0	9.8	....
Mar. 22 24	25.8	25.0	26.4	0.0	12.4	....
Steer D:						
Jan. 9 to 12	24.4	[2]0.0	35.4	0.0	11.4	7.2
Jan. 17 19	28.0	22.6	30.0	0.0	11.4	....
Jan. 25 27	33.2	16.6	29.4	0.0	9.4	....
Feb. 1 3	25.4	28.6	34.2	0.0	10.2	....
Feb. 8 10	24.0	16.8	19.6	0.0	8.4	....
Feb. 14 16	32.0	22.6	21.6	0.0	0.0	....
Feb. 22 24	21.4	17.2	32.8	0.0	0.0	....
Mar. 5 7	24.0	26.4	25.4	0.0	0.0	....
Mar. 13 15	18.6	28.4	20.8	0.0	11.6	....
Mar. 20 22	25.0	25.8	27.0	0.0	11.2	....

[1] The first day of fasting began at 2 p. m., the last feed having been given between 7 and 8 a. m. of that day. The water was drunk at 2 p. m., at the beginning of each day.

[2] Steer fasted for standard metabolism experiment, but experiment was not made.

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[a] Benedict, Carnegie Inst. Wash. Pub. No. 203, 1915, p. 84.

[b] Kellner, Die Ernährung der landwirtschaftlichen Nutztiere, 9th ed., Berlin, 1920, p. 185.

[c] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 114.

for long periods. In view of the uncertainty as to the water needs of fasting steers, however, it seemed best not to attempt to control the amount of water consumed, or, indeed, to withhold water entirely, but to permit the animals to drink voluntarily each day.

The irregularity in the water consumption of animals, particularly during fasting, made it desirable to secure weights of the water actually consumed. For this reason the animal was weighed immediately before and after drinking and the tub of water was likewise weighed. The time of drinking and the temperature of the water were both recorded, as it is now being recognized more clearly that the introduction of very cold water, particularly in large quantities, into an animal's alimentary tract makes heavy demands upon its store of heat and undoubtedly profoundly inhibits the activity of the alimentary tract. In most of these fasts precautions were taken to have the temperature of the water not far from 15° to 20° C., for in much of our previous work on submaintenance feeding the water was extremely cold, at times being but 1 or 2 degrees above 0° C.[a]

In studying fasting conditions it would be advantageous to know exactly the salt-content of the drinking-water. This was not determined. The water used was obtained from the university water system, supplied by a deep well. It was frequently analyzed and found to be of a high degree of purity. Theoretically, of course, it would have been better to have given the animals only distilled water, as was done in the long study of the fasting man made by the Nutrition Laboratory.[b]

Records of the water consumed by the steers prior to and during the series of 2-day fasts in 1923 are given in Table 18 and similar records for the longer fasts are given in Table 19.

The picture of the water consumption on the three days with feed prior to the short fasts in 1923 gives a reasonably close indication of the normal water consumption of these animals when living at an essentially uniform nutritive plane, upon a constant ration. Thus, during the feeding-periods from January to April 1923 the animals received daily 9 kg. of hay and 2 kg. of a meal mixture made up of equal parts, by weight, of corn meal, linseed meal, and wheat bran. On this feed the consumption of water was usually reasonably constant, amounting to not far from 20 to 25 kg. per day. There is a marked exception in the case of steer D on the second day before the fast of January 9 to 12, 1923. On this day the afternoon ration of hay and meal had been withheld, as it was planned to carry out an experiment in the respiration chamber the next morning. No experiment was made, however. At 2 p. m. on this day steer D consumed no water. A possible explanation for this will be given later (see p. 79).

Prior to the longer fasts of 5 to 14 days, the animals were on varying nutritive planes and hence drank varying amounts of water and consumed varying amounts of feed before the fasts. This fact must be taken into consideration in interpreting the records for water consumption in the longer fasts reported in Table 19. During the three days with feed prior to the first four fasts the daily water consumption was usually not far from 30 to

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 112.

[b] Benedict, Carnegie Inst. Wash. Pub. No. 203, 1915, p. 85.

TABLE 19.—*Daily water consumption prior to and during fasts of 5 to 14 days*[1]

Steer and dates of fasts	Days before fast			Days fasting													
	3	2	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	kg.	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*
Steer C:																	
Dec. 6 to 13, 1921...	17.4	26.6	21.6	17.6	0.0	0.0	0.4	7.8	1.4	0.4	......	......	......	......	......	......	......
Jan. 4 14, 1922...	30.4	33.8	44.6	36.4	0.0	7.0	0.0	1.8	10.6	0.0	2.6	8.0	0.0	......	......	......	......
Apr. 17 May 1, 1922	32.8	34.4	33.6	32.0	12.4	4.6	0.0	3.8	9.6	0.2	4.4	3.2	4.6	5.2	0.0	2.2	4.8
June 1 7, 1922...	38.6	38.8	40.2	37.8	10.6	0.6	0.0	13.4	0.0	......	......	......	......	......	......	......	......
Nov. 6 16, 1922...	......	......	......	0.0	0.0	10.2	0.0	0.0	3.2	1.2	6.8	0.0	......	......	......	......	......
Nov. 4 10, 1923...	......	......	......	......	0.0	0.0	0.0	0.0	......	......	......	......	......	......	......	......	......
Mar. 3 13, 1924...	9.8	12.4	10.4	9.6	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.4	0.0	......	......	......	......
Steer D:																	
Dec. 6 to 13, 1921...	31.0	24.4	25.2	18.6	0.0	0.4	13.6	0.0	0.0	13.0	......	......	......	......	......	......	......
Jan. 4 14, 1922...	32.2	32.8	35.0	43.4	0.0	10.0	0.0	18.0	0.0	9.4	0.0	3.6	9.6	......	......	......	......
Apr. 17 May 1, 1922	31.8	31.8	29.6	32.4	7.8	8.4	5.2	0.0	7.8	0.0	6.8	4.8	8.4	0.0	6.8	4.4	0.0
June 1 6, 1922...	36.0	38.6	35.6	36.6	0.6	13.6	0.0	21.0	......	......	......	......	......	......	......	......	......
Nov. 6 14, 1922...	......	......	......	0.0	13.2	5.0	3.6	24.4	0.0	0.0	......	......	......	......	......	......	......
Nov. 4 9, 1923...	......	......	......	......	0.0	0.0	16.8	3.4	......	......	......	......	......	......	......	......	......
Mar. 3 12, 1924...	14.2	11.4	12.8	11.2	0.0	0.0	11.8	0.0	0.0	11.2	0.0	0.0	......	......	......	......	......
Steer E:																	
Feb. 12 to 17, 1924...	10.0	2.4	10.0	2.4	6.2	1.8	8.0	......	......	......	......	......	......	......	......	......	......
Steer F:																	
Feb. 12 to 18, 1924...	10.0	1.4	12.2	0.0	0.0	0.0	2.8	2.4	......	......	......	......	......	......	......	......	......

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[1] The values given in this table represent the water drunk at the beginning of the day.

35 kg., varying somewhat with the animal, the records for both steer C and steer D prior to the first experiment in December 1921 being somewhat lower than any of the others. The ration prior to these fasts was an essentially maintenance ration of hay and meal. Particular attention should be paid to the records of water consumption preceding the two fasting experiments in March 1924, with steers C and D, and the two experiments in February 1924, with steers E and F. In these instances all four animals were on a distinctly submaintenance plane of nutrition and had been consuming regularly less water than they had under normal conditions.

During the first day of fasting the intestinal tract of the steer, which has been receiving maintenance rations, may still contain a large amount of feed, which has not been entirely digested or absorbed, and which needs water for its further hydration. The amount of water consumed on the first day of fasting is therefore of unusual interest.

From Table 18 it will be seen that in every instance the animals drank no water at the beginning of the first fasting day, although they were offered water and had actually been without feed only for 6 hours. At the beginning of the second day of the fast, or the end of the first day, when no feed had been eaten for about 30 hours, steer C drank water on every occasion and steer D on all but three occasions. Indeed, the amount of water taken was reasonably uniform at about 9 or 10 kg. In the one experiment with both animals which lasted for 3 days the amount of water consumed decreased on the third day to 6 and 7 kg., respectively.

In the longer fasts, in contradistinction to the short fasts, the animals drank water in all but three instances at the beginning of the first day of fasting, but there are numerous instances when no water was consumed at the beginning of the second day of fasting. The data for water consumption during the 4-day experiments with steers E and F in 1924 and 1925 also show that the animal drank water at the beginning of the first day of fasting, but sometimes did not drink at the beginning of the second day. This difference in the picture presented by the short fasts and that presented by the longer fasts and the fasts in 1924 and 1925 is probably due to several factors. Thus, the difference in environmental temperature may have been one cause of the difference in water consumption. The longer fasts were made at relatively high environmental temperatures, and no attempt was made to alter the temperature during the fast. In the short fasts, on the contrary, the effect of both high and low environmental temperatures was studied, the animal being occasionally subjected to a low temperature on one day and to a much higher temperature on the very next day, or vice versa. During the period of 2-day fasts, moreover, there were such short intervals of feeding between the fasts that the animals probably did not have time to recuperate entirely from one fast before another was started. Thus, the animals were fasted approximately once a week, and there was almost a continuous rhythm of temporary digestive disturbance, due to the fasting, with irregularity of water intake following the fast. On the first day or so after the fast the water consumption was low, but there was a tendency to make up for this in the subsequent days and a high water consumption was reached after 4 or 5 days. The animal was then apt to refuse water for a day. By pure coincidence, so far as is known, this seeming rhythm in water consumption due to the intermittent fasting happened to correspond with the fasting schedule.

The records for the water consumption in the experiments made in 1924 and 1925 were for steers E and F, whereas the records for the earlier fasts were chiefly with steers C and D. In these later experiments steers E and F were kept for 4 days continuously inside the respiration chamber. The experimental conditions were therefore distinctly different from the stall conditions obtaining in the series of long and short fasts, in that the animal when inside the respiration chamber is in an atmosphere of much higher humidity, necessitated by the lower ventilation, than he is when outside the chamber in his stall. Consequently the data for drinking-water obtained in the later experiments are not strictly comparable with those obtained in the long and short fasts. It should be pointed out, however, that one would expect that the days when the animal would not drink would be the days when he was inside the chamber, when the humidity was high, and the experiments in 1924 and 1925 show that this was not the case, thus suggesting that the humidity had but little effect on the loss of moisture from the lungs and skin.

The data for the water consumption during the progress of the fast indicate that at the beginning of the second day no water was consumed in ten instances, although as much as 10 to 13 kg. were taken in three instances. On the third day there was a disposition to a return to water consumption. On the fourth day steer C drank no water except in the fast in December 1921, when he took 0.4 kg. With steer D, however, the water consumption on the fourth day of fasting varied from 0.0 to as high as 16.8 kg. On the fifth day irregularity in the different experiments is again shown, large amounts being sometimes taken by steer D. On the sixth day and the following days the water intake is irregular.

No long periods of complete refusal of water are noted, save in the experiment with steer C after pasture in November 1923, when for 4 days he drank no water, and in the experiment in March 1924, after submaintenance feeding, when steer C drank practically no water for 10 days, if one excepts the 0.2 kg. taken on the seventh day and the 1.4 kg. taken on the ninth day. Steer D drank no water in the March experiment following submaintenance feeding, except on the fourth and seventh days, when 11 kg. were taken. Steer E, which fasted after submaintenance feeding, drank small amounts of water during the entire fast, and steer F, also fasting on a low nutritive plane, drank no water at all for three days.

In general, distinctly less water was consumed by both steer C and steer D when fasting after submaintenance feeding or after pasture than when fasting on a higher nutritive plane. Probably the large amount of water in the succulent grass, or perhaps the possibility that the steers had been drinking just prior to leaving pasture, may have contributed a plentiful amount of water to the animal's organism at the time of the fasts off pasture. One may conclude, therefore, that when steers are liberally supplied with water, as on pasture feeding, the extra water demands of the body are relatively small and for several days little or no water may be taken. Similarly, when the animals are on a low nutritive plane and receiving a small ration of hay, there may be a long period of time when no water or very little water is taken. The inference is that drinking-water might be withheld from steers during a fast, especially under conditions of submaintenance feeding and probably after pasturage, without detriment to the animal. The long periods of complete abstinence from water while fasting, noted especially with steer C, are strikingly similar to experiences in fasting experiments made with dogs. In such cases the fasting steer is practically a carnivorous animal, subsisting upon its own flesh and not requiring any appreciable amount of water to maintain its water-balance, for little or no water was taken during the later stages of fasting, although water was offered every day.

In connection with the feeding of these steers, certain definite observations regarding the consumption of water can be recorded. When the steers were fed both morning and evening and were offered water at 2 p. m., that is, between the two meal times, they usually drank. If the afternoon feed and the following morning's feed were withheld, they usually did not drink at 2 p. m. the next day. In those few instances when they did drink after both feeds had been withheld, a large volume of urine was excreted during the next 24 hours. This observation belongs, more strictly speaking, in the section discussing the volume of urine, but is introduced here simply to show the immediate effect of water consumption upon the output of urine when the daily ration is withheld and there is not a corresponding supply of dry matter of feed to absorb the water.

In none of these fasting experiments was salt given. The animals had to rely solely upon the salt normally present in the drinking-water, an analysis of which shows that they received a very small amount of mineral matter from this source.

A general inspection of the detailed records secured during this research shows that when the steers are fed hay and meal, the amount of water consumed bears a fairly close relationship to the total intake of dry matter in the ration.

FECES

The differences in the amounts of feces excreted by the dog, by man, and by the ruminant are in large part explained by the nature of their intestinal tracts and particularly by the nature of their food. The residue or fill in the intestinal tract of the ruminant is very large, amounting at times to over 20 per cent[a] of the animal's weight, whereas the intestinal residue in the case of man or the dog is small. Fasting dogs frequently pass no feces for a long period. Indeed, the man who fasted at the Nutrition Laboratory for 31 days passed no feces during the entire time.[b] The large intestinal content or ballast of the steer, however, although for some little time subject to digestive processes and to fermentations, must be expelled, because a large part of it is not digested by the animal organism. A study of the feces of these fasting steers was therefore made for the purpose of securing

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 107 and 108.

[b] Benedict, Carnegie Inst. Wash. Pub. No. 203, 1915, p. 230.

information on several points: first, regarding the actual mass of feces passed, particularly with reference to the length of the fast; second, regarding the effect of the previous ration upon this mass; and third, regarding the chemical composition of the feces as influenced both by fasting and by the previous ration.

Amount and Frequency of Defecations

Earlier experience with steers during undernutrition showed that extensive changes in the physical appearance of feces were not accompanied by great alterations in the moisture-content. It is deemed permissible, therefore, to discuss the fecal excretion of these fasting steers on the basis of the fresh weight and to defer for the moment a consideration of the amount of dry matter, which involves a knowledge of the water-content.

Due to the irregularity in the expulsion of feces by all cattle, the individual defecations should be weighed separately. To have an attendant constantly at hand to collect the feces, as dropped, is perhaps the simplest method, but it is expensive. Many experimenters have had recourse to various types of ducts, either of rubber or oiled silk, to conduct the feces, as passed, into reasonably air-tight containers. The small number on our experimental staff would not permit the first of these methods of collection, and the second method would not have much advantage over the simple form of trap shown in a previous report,[a] through which the feces drop directly into convenient receptacles below. When the animals are fairly well fed this latter method is ideally simple and is probably subject to no great error, for the losses from vaporization are relatively small in proportion to the total weight of feces. On the other hand, in the weighing of the very small amounts of feces occurring during undernutrition, and particularly during fasting, the error may be relatively larger. Any losses in weight would, however, undoubtedly be in large part due simply to vaporization of water, although a loss of ammonia may take place even if the feces stand in a can for only a few hours.

The weight of fresh feces voided each day during the fasts of 5 to 14 days and the average daily weight of feces for a week with feed preceding each of these fasts have been tabulated in Table 20. These daily weights, however, do not represent exact 24-hour separations. The steers did not voluntarily defecate exactly at a given moment. The feces cans were removed each day at 2 p. m., but feces might have been passed either immediately before 2 p. m. or several hours before, and the actual time between the first and last defecation on any given date may be longer or shorter than 24 hours. It was possible, therefore, only to approximate the true daily excretion by making the collections in 24-hour periods, and it seems inadvisable to attempt to compute the hourly rate.

As pointed out in an earlier report,[b] the fecal excretion is notably affected by the character and the amount of the ration. The most pronounced factor affecting the character and the amount of feces is clearly the bulk of fibrous material, hay, rather than the amount of meal, although it is common

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 31.

[b] *Ibid.*, pp. 121 et seq.

TABLE 20.—*Daily excretion of fresh feces before and during fasts of 5 to 14 days*

Steer and dates of fasts	Average daily feces week before fast	Days fasting													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Steer C:	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*
Dec. 6 to 13, 1921	21.50	19.46	8.19	6.60	1.87	1.98	1.80	1.43	......	......	......	......	......	......	......
Jan. 4 14, 1922	23.93	20.90	9.00	4.96	1.72	2.43	2.56	2.52	0.82	0.56	0.62	......	......	......	......
Apr. 17 May 1, 1922	24.92	20.43	7.08	4.82	3.95	2.91	3.35	2.25	3.22	1.28	0.69	2.60	1.21	1.14	0.92
June 1 7, 1922	28.39	24.34	10.66	7.42	2.33	3.59	1.59	......	......	......	......	......	......	......	......
Nov. 6 16, 1922	......	13.42	6.53	3.17	2.72	1.52	1.38	0.89	1.83	1.18	......	......	......	......	......
Nov. 4 10, 1923	......	......	16.83	10.15	4.88	3.00	......	......	......	......	......	......	......	......	......
Mar. 3 13, 1924	7.30	[1] 5.20	2.89	3.86	1.81	1.51	0.25	0.72	0.67	0.47	0.00	......	......	......	......
Steer D:															
Dec. 6 to 13, 1921	19.12	18.94	4.81	1.93	3.90	1.59	2.31	1.83	......	......	......	......	......	......	......
Jan. 4 14, 1922	21.49	18.21	7.86	3.30	2.36	2.29	1.18	1.58	1.52	0.77	0.81	......	......	......	......
Apr. 17 May 1, 1922	22.52	19.06	7.42	5.47	3.81	1.42	2.54	1.81	1.39	1.32	1.25	1.33	1.39	1.08	0.63
June 1 6, 1922	28.83	20.76	8.64	5.71	2.20	3.17	......	......	......	......	......	......	......	......	......
Nov. 6 14, 1922	......	13.54	5.26	4.70	1.04	2.58	0.84	1.74	0.19	......	......	......	......	......	......
Nov. 4 9, 1923	......	......	16.63	7.52	3.66	4.14	......	......	......	......	......	......	......	......	......
Mar. 3 12, 1924	7.22	[1] 5.00	4.19	3.51	1.57	2.29	0.90	0.92	1.09	0.79	......	......	......	......	......
Steer E:															
Feb. 12 to 17, 1924	4.62	3.28	3.78	2.13	1.13	0.45	......	......	......	......	......	......	......	......	......
Steer F:															
Feb. 12 to 18, 1924	4.37	4.25	2.35	2.44	1.34	0.75	0.52	......	......	......	......	......	......	......	......

[1] This value represents a period of collection of only 17 hours, from 2 p. m., Mar. 3, to 7 a. m., Mar. 4.

experience that the feeding of meal in large amounts, particularly oil meal, has a tendency to scour animals and results in more watery and voluminous feces.

An examination of the data obtained during the feeding-periods shows that in general the weight of fresh feces is twice that of the ration. Thus, during the periods of feeding in 1921 and 1922, when about 9 kg. of hay and from 2 to 6 kg. of meal were consumed daily, 24 kg. of feces were passed daily on the average both by steer C and by steer D. From January to April 1923 these steers also received a maintenance ration of hay and meal, but the food intake was disturbed by the numerous short periods of fasting and the average weight of feces passed daily during the feeding periods was therefore somewhat smaller than in the earlier maintenance periods. The marked reduction in ration prior to the fast in March 1924 was instantly reflected in a pronouncedly lower fecal expulsion. Thus, steers C and D had been receiving daily only 4.5 kg. of hay and no meal, and as a result the average daily amount of feces was only about 7 kg., i. e., still nearly twice as great as the ration. A similar picture is noted with steers E and F on a submaintenance ration of 2.5 kg. of hay and 100 gm. of meal in February 1924, when their daily fecal excretion averaged about 4.5 kg. It is especially worthy of note that both the younger and the older animals, considered as duplicates or pairs, showed much the same reaction to the ration, as exemplified by the amount of feces excreted.

There is a tendency for the daily fecal excretion of steer D to be slightly smaller than that of steer C. Indeed, detailed records for almost every day from November 26, 1921, through January 5, 1923, show that on the average steer D excreted 14.81 kg. of feces per day and steer C 15.42 kg., although both animals received the same treatment, side by side in the same stalls, were subjected to the same number of respiration experiments, consumed the same amount of food, and drank the same amount of water (21.7 kg., steer C; 21.5 kg., steer D).

In the case of all four steers, the collection of feces for the first day of fasting began at 2 p. m., at which time the feces containers were replaced with empty containers. The last feed prior to the fast was given in the morning between 6 and 8 o'clock. Hence the weights of feces reported for the first day of fasting represent a 24-hour period beginning about 6 or 8 hours after the last feed. The weights of feces reported for the first day of the March 1924 fast, however, represent only a 17-hour period from 2 p. m. to 7 a. m., as it was decided on the second day to have the 24-hour periods begin at 7 a. m. instead of at 2 p. m. In the two November fasts following pasture it was not easy to determine exactly when the animals had last eaten. The weights of feces reported for the first day of the November 1922 fast represent a period beginning 6 hours after the steers were brought in from pasture. In the November 1923 fast the collection of feces did not begin until 22 hours after the steers had been brought in from pasture, and the first 24-hour collection of feces during this fast is therefore attributed to the second day.

On the first day of fasting there was a decrease in the amount of feces passed, although in most instances this decrease was not pronounced. In the special series of 2-day fasts during January, February, and March 1923, the data secured regarding the excretion of feces support this view. In this series, in which all the fasts followed maintenance feeding, approximately 19 kg. of feces were passed daily on the average during the week prior to the fast. On the first day of fasting there was a general average decrease to 16 kg., or a fall of 16 per cent. On the second day of fasting the average expulsion amounted to 6 kg. The total average amount for the first two days of fasting is therefore about 22 kg. or essentially that passed daily during the feeding-period. This finding, that the total amount of feces passed during the first two days of fasting is approximately equal to the amount passed daily during the feeding-period preceding it, is also true in the case of the longer fasts reported in Table 20, both those following maintenance feeding and those following submaintenance feeding. In the case of the fasts following pasture, obviously no records for the feeding-period were available.

The first four long fasts of steers C and D are comparable, because they followed an essentially maintenance ration. The fecal excretion on the first and second days of these fasts is larger than the excretion noted in the short fasts in 1923. Thus, both steers excreted approximately 24 kg. during the week on feed before the fasts and on the average not far from 20 kg. of feces on the first day of these four fasts. The average percentage decrease on the first day, however, is practically the same as was noted in the 1923 series, i. e., 17 per cent. This relatively small average decrease of 4 kg. is perhaps surprising, but one should recall that feed was actually eaten 8 hours prior to the collection of feces for the first fasting day. This fact, coupled with the large ballast in the intestinal tract, minimizes any immediate effect of fasting upon the fecal discharge.

In general, the larger amounts of feces prior to these four fasts are followed by larger amounts of feces on the first fasting day. In the April fast of steer C and the June fast of steers C and D, decreases in fecal excretion of from 4 to 8 kg. were noted on the first day, but in the other fasts the decrease is more nearly 2 or 3 kg. With the large bulk of fecal matter in the intestinal tract and the irregularity of defecation, it is perhaps not surprising that the fecal output on the first day is not more uniform. The length of time intervening between the last ingestion of feed and the beginning of the first day of fasting and the amount of the last ration received prior to the fast should also be considered in this connection. Thus, somewhat larger amounts of meal were eaten prior to the fasts in January, April, and June 1922 than were eaten prior to the fast in December 1921, and in all but one instance the fecal excretion in these experiments is larger than that noted in the December experiment. The large amount of meal eaten prior to the fast in January 1922 did not have a pronounced effect upon the fecal excretion either before the fast or on the first day of fasting in the case of steer D, but in the case of steer C the amounts of feces are somewhat larger than in the 1921 experiment, when less meal was eaten. Before the fast in June 1922, when both steers had been receiving about 8.5 kg. of hay and 4 kg. of meal daily, there was a distinct increase in the average fecal output on feed and the largest amounts of feces on the first day were noted in this fast.

After pasture the feces are much smaller in amount. In the fast in November 1922 both steers voided only 13.5 kg. on the first day. In the fast in November 1923 the feces were not collected until the second day, but the average amount on the second day, 16.7 kg., is actually greater than that observed on the first day and about three times as great as that recorded on the second day of the 1922 fast following pasture. Irregularity in pasture feeding makes sharp conclusions impracticable.

In the fasts following undernutrition in 1924 the decrease in feces on the first day is small with all four animals, but likewise the initial amounts on feed are small. The fecal discharge on the first day of fasting is, however, very small when compared with the amounts voided in the other fasts following maintenance rations or pasture feeding.

Inspection of the data for feces on feed and on the first two days of fasting shows in general, therefore, that the decrease in feces on the first day of fasting is small following maintenance feeding. After submaintenance feeding the decrease is small and the total amount involved is likewise small. In the case of steers E and F the total amount on the first day is small, both because the fasting followed submaintenance feeding and because the animals were small.

Because of the continually decreasing ballast and the extensive changes in the amount of water intake during fasting, great differences in the frequency of defecation, the amount of each defecation, and the total amount per day are to be expected. Only the total amount per day is considered in Table 20. Records were kept, however, of the amount and time of each defecation during all of the fasts reported in Table 20, except that in December 1921. These records show that in the fasts following maintenance feeding the number of defecations on the first day was fairly large, varying from 9 to 12 defecations during the day. In the two November fasts after pasture the defecations on the first day decreased to 5 or 6 in number. In the fasts following submaintenance rations steers C and D voided feces at five or six different times during the first day and steer E at four different times. On the other hand, with steer F there were nine defecations, all reasonably uniform in size. Aside from this one instance, however, the number of defecations on the first day of fasting was less following pasture or submaintenance feeding than following maintenance feeding with hay or with hay and meal.

The frequency of defecation and the actual amount of each defecation is best shown graphically. Accordingly, the data for the individual defecations have been plotted for three typical fasts of steers C and D, namely, the 14-day fast in April 1922, the 9-day fast after pasture in November 1922, and the 10-day fast after submaintenance feeding in March 1924. (See Fig. 4.) The total daily excretions are recorded upon the chart in the top row of figures above each curve, thus duplicating the data in Table 20 for these three fasts.

In the 14-day fast in April, which followed maintenance feeding of 9 kg. of hay and 3 kg. of meal daily, the number of defecations and the amount of each defecation were large with both animals on the first day. On the second day there are fewer defecations and the total mass is much smaller.

The charted data for this fast show a distinctly downward trend both in the number of defecations and the amount of each defecation until about the seventh day. After the seventh day there are a large number of small defecations daily. This is particularly true of steer D, whose total daily fecal discharge on the average is actually not quite so large as is that of steer C. On the last day of the fast, for example, steer D had 11 defecations, practically all under 100 grams each.

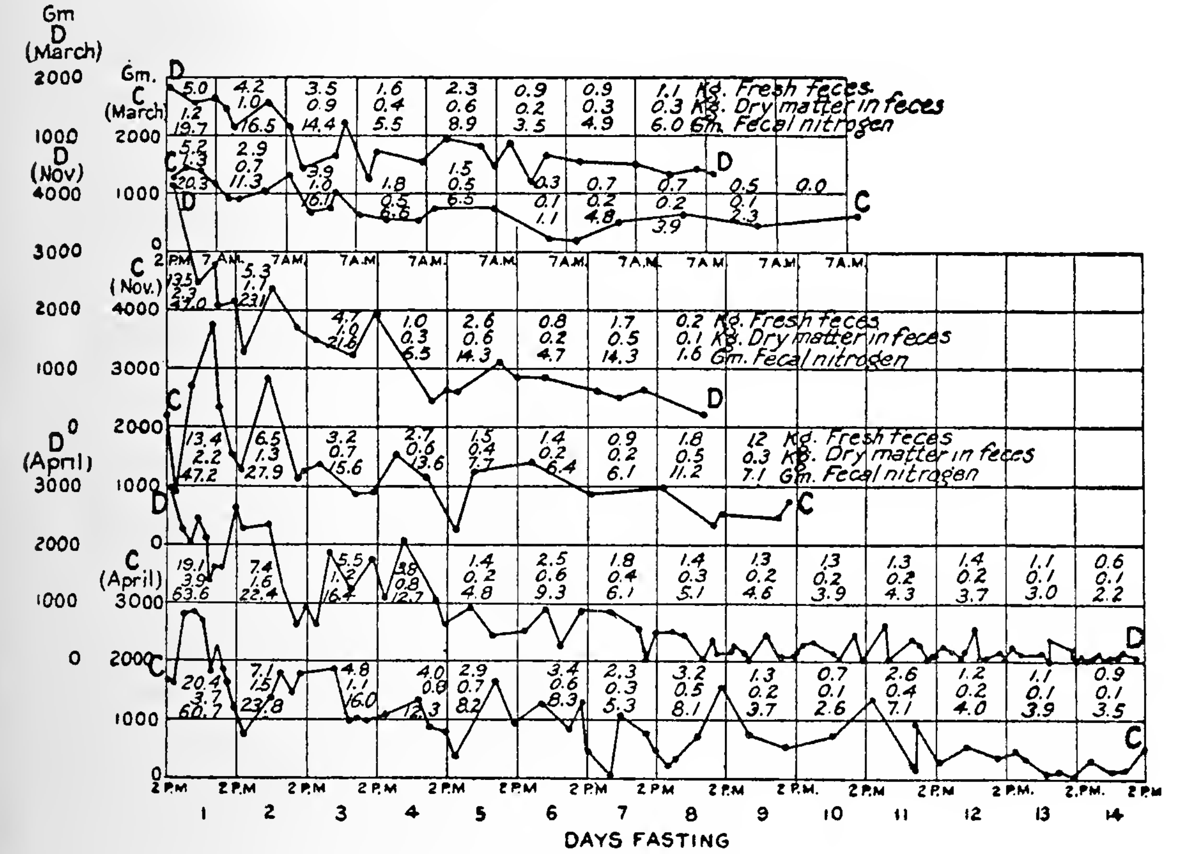

Fig. 4.—Individual defecations of steers C and D during fasts in April and November 1922, and March 1924

The two curves at the bottom of the chart represent the fasts in April 1922, which followed a maintenance ration of 9 kg. of hay and 3 kg. of meal. The two curves in the middle are for the November fasts, which followed pasture feeding. The two curves at the top are for the March fasts, which followed a submaintenance ration of 4.5 kg. of hay. The figures in the top row against each curve represent the total daily weights of fresh feces in kilograms, those in the middle row the kilograms of dry matter in feces per day, and those in the bottom row the grams of fecal nitrogen per day.

A relationship between the amount of water consumed per day and the consistency and the amount of feces passed has been observed frequently, both in our series of undernutrition and of fasting experiments. It is not unlikely that some of the irregularities shown in Fig. 4 are due to differences in water intake. In no instance, however, is a striking effect of the water consumption upon the mass of feces indicated on any given day. Reference to the data for water consumption (see Table 19, p. 78) shows, for example, that on the eleventh day of this April fast steer C passed a relatively large amount of feces, 2.6 kg., and drank 5.2 kg. of water. Steer D, on the other hand, drank 8.4 kg. of water on the tenth day of this fast, but there was practically no change in the weight of fresh feces.

The daily excretion is usually somewhat less than half as much on the second day as on the first, save in the March fast after submaintenance feeding. The total daily amount falls off fairly regularly thereafter, but from the fifth day on the average excretion of all animals is not far from 1.5 kg. per day. Feces were passed upon every day of the fasting experiments, with the single exception of the tenth day in the March 1924 fast of steer C, after submaintenance feeding. It is clear that the previous plane of nutrition, particularly the submaintenance plane, affects the fecal excretion. The influence of pasture feeding is noticeable only for about 3 days, although the amounts of feces excreted by both steers during the fast in November 1923 were large even after the third day, indeed larger than in most of the other fasts.

A quantitative study of either the total daily amounts of feces or, indeed, the dry matter of feces, must take into account the fact that the defecations of these animals are involuntary, the ballast is very large, and considerable differences in water intake occur. Only the most general conclusions regarding the amount and rate of defecations are, therefore, justifiable, for undoubtedly complications are introduced by the water intake, the character of the feed (relative proportion of coarse fiber and concentrates), and the time elapsing between the last feeding and the beginning of the collection of feces.

It is perhaps to be regretted that no provision could be made for the separation of feces, particularly by the chromic oxide method of Edin.[a] This seemed impracticable, and doubtless the marker would have been retained throughout the entire fasting period. The use of a foreign substance to mark the feces in ruminants has always been considered unsatisfactory. The elaborate study of Ewing and Smith,[b] who used rubber disks to indicate the rate of passage of food residues through the steer, showed that some of the rubbers remained in the animals for 60 days, indeed until they were slaughtered. Hence Ewing and Smith conclude that such a method of marking is unreliable. The gross contents of the alimentary tract of steers is well illustrated in their report. Thus, they find that with 6 steers, weighing on the average 380 kg., the gross contents of the intestinal tract varied from 36.6 to 70.8 kg.; 5 of the 6 steers had a residue of 60 kg. or more. The percentage of dry matter in these contents varied from 6.07 to 12.92, averaging not far from 9 per cent. The authors conclude that the time required for the ordinary ration to pass through the intestinal tract probably varies between 72 and 84 hours, the rate of passage being largely influenced by the nature and the quantity of the ration, the importance of the two influencing factors being in the order named.

The picture shown by steers E and F is in accord with that of the two large animals, if one takes into account the fact that they are smaller and that they had been upon a submaintenance ration. It is singular, however, that the daily weights of feces of each of these smaller steers during their fast following submaintenance feeding should be essentially the same as were noted with the larger animals when fasting after a submaintenance

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[a] Edin, Nordiske Jordbrugsforskeres Forenings, Kongres i København, July, 1921, p. 388.
[b] Ewing and Smith, Journ. Agric. Research, 1917, 10, p. 55.

FIG. 5.—Feces voided by steer C on the sixth day of fasting, November 10, 1923
The rule is 15 inches (38 cm.) long

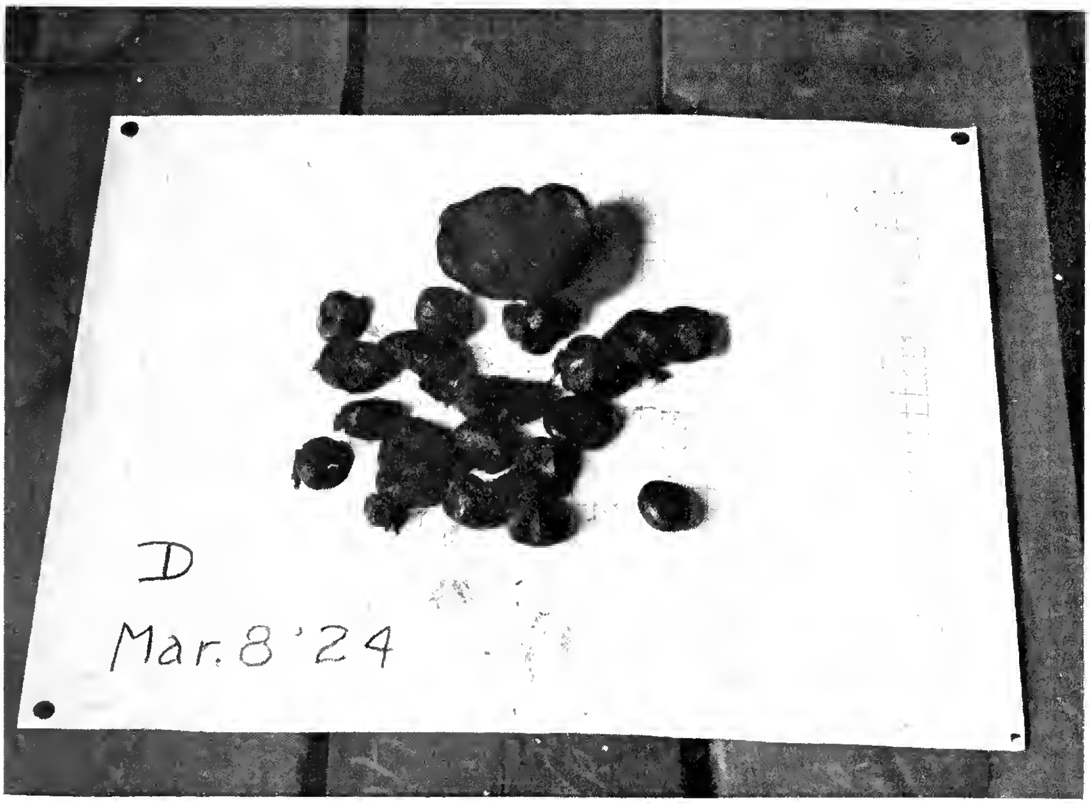

FIG. 6.—Feces voided by steer D on the fifth day of fasting, March 8, 1924
The squares are in inches, or about 2.5 cm.

ration. Thus, although prior to these fasts steers C and D excreted approximately 7 kg. of feces per day and steers E and F only about 4.5 kg., during fasting the total 24-hour excretions after the first day are much more nearly uniform.

The data in Table 20 and in Fig. 4 indicate clearly that fasting greatly reduces the fecal excretion, which, however, continues throughout the entire fast, irrespective of its length. The previous plane of nutrition affects the total daily amounts, and even after pasture the fill and fecal excretion during the fast remain at a relatively high level. With at least one steer the frequency of defecation greatly increased toward the end of the fast.

Physical Characteristics of Feces

In an earlier report[a] attention was called to the striking differences in the characteristics of the feces when the animals were upon submaintenance rations and when upon full feed. In the latter instance the feces were semifluid, would not hold form, and were very bulky. When the steers were upon submaintenance rations, their feces became much harder and more pilular in form, resembling in many instances the feces of a horse. The determinations of water in these feces did not show so great a difference in the percentage of moisture as would be expected from the striking difference in physical appearance. Indeed, a difference of only 2 or 3 per cent in the water-content was noted. It seemed incredible that this small percentage difference in water-content could be accompanied by such a great difference in the physical configuration of the feces. In connection with the study of fasting steers opportunity was had to confirm this observation, for steers C, D, E, and F were at varying times upon submaintenance rations. During their submaintenance feeding, similar changes in the physical characteristics of the feces were noted, and the chemical analyses, especially the water determinations, show that these great changes can take place without appreciable alterations in the water-content.

Comments of the observers regarding the physical characteristics of the feces during the 14-day fast in April 1922 are typical of the physical characteristics of the feces in practically all of the fasts. The feces at the beginning of the fast in April 1922 were soft and very plastic, as would normally be expected from a ration containing 3 kg. of a meal mixture having a relatively large proportion of linseed meal and bran. As the amount of feces decreased during the progress of the fast, the feces became visibly firmer, taking on a dry, pilular form by the fifth day. By the eighth day the consistency of the feces became more variable, some passages being firm and fibrous in appearance, and others, especially those passed in the respiration chamber, being soft. This latter condition was more marked with steer C. Variability in the physical consistency of the feces, especially in the latter periods of fasting, is noted likewise in the water-content of the feces, strikingly high percentages of water being found. (See Table 21, p. 90.) The extremely dry, pilular form which fasting feces may assume is excellently illustrated in Figs. 5 and 6, which show the feces of steer C on November 10, 1923, the sixth day of the fast, and of steer D on March 8, 1924, the fifth day of the fast following submaintenance feeding.

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 125.

TABLE 21.—*Percentage of dry matter in feces during fasts of 5 to 14 days*

Steer and dates of fasts	Days fasting														Composite sample for entire fast
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Steer C:															
Dec. 6 to 13, 1921	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	19.4
Jan. 4 14, 1922	16.7	19.1	17.3	21.7	17.9	16.2	15.5	21.7	18.5	20.4	.....	.....	.....	.....	17.9
Apr. 17 May 1, 1922	18.3	21.3	22.7	19.5	23.1	17.1	12.5	14.1	16.9	17.2	13.8	14.6	13.0	15.1	16.8
June 1 7, 1922	16.7	17.3	16.8	18.4	14.5	.....	.....	.....	.....	.....	.....	.....	.....	.....	16.7
Nov. 6 16, 1922	16.5	20.2	23.4	22.8	23.0	17.4	27.4	26.8	26.3	.....	.....	.....	.....	.....	.....
Nov. 4 10, 1923	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	20.1
Mar. 3 13, 1924	24.3	26.7		27.6	29.8		28.7	33.2	26.2	([1])	.....	.....	.....	.....	26.7
Steer D:															
Dec. 6 to 13, 1921	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	19.8
Jan. 4 14, 1922	17.9	26.7	19.9	20.6	21.3	25.4	22.3	15.5	20.6	15.6	.....	.....	.....	.....	19.5
Apr. 17 May 1, 1922	20.5	21.8	21.5	19.7	17.6	23.4	20.2	18.6	16.4	15.8	16.1	13.0	13.3	13.5	19.2
June 1 6, 1922	17.1	17.2	17.4	18.6	17.3	.....	.....	.....	.....	.....	.....	.....	.....	.....	17.0
Nov. 6 14, 1922	16.7	21.5	22.1	28.7	24.4	27.0	29.6	37.1	.....	.....	.....	.....	.....	.....	.....
Nov. 4 9, 1923	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	19.5
Mar. 3 12, 1924	23.1		24.8	24.2	26.0		33.7	29.3	26.7	.....	.....	.....	.....	.....	25.1
Steer E:															
Feb. 12 to 17, 1924	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	21.0
Steer F:															
Feb. 12 to 18, 1924	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	22.9

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[1] There were no defecations between 7 a. m., Mar. 12, and 7 a. m., Mar. 13, but 0.62 kg. of feces were passed in the respiration chamber between $7^h 10^m$ and $10^h 25^m$ a. m., Mar. 13, before the steer was fed. The dry matter in these feces was 20.6 p. ct.

Another pronounced characteristic of the feces during the fasting experiments was an exceedingly offensive odor, which frequently was noticed toward the end of the fast.

Chemical Composition of Feces

The difficulty of avoiding loss of moisture and frequently of nitrogen (ammonia) in the drying of feces made it necessary to determine the nitrogen-content directly in fresh feces. The water-content was determined by subjecting a sample of approximately 10 gm. of fresh feces to the usual process of drying. With but few exceptions these two determinations were made on each day's collection of feces during the long fasts and on a composite sample of the feces passed during the entire fasting-period, as well as on a composite sample of feces passed during the feeding-periods just preceding and following the fasts. No correction was made for loss of material. Further analyses of the feces were impracticable, and the study of the chemical composition of fasting feces is confined solely to the analyses of the water-content and the nitrogen-content.

Dry Matter in Feces

The marked changes in the physical appearance of the feces made the determinations of water-content especially interesting, in view of the lack of correlation between major changes in physical appearance and changes in water-content previously noted in the undernutrition study with steers. The percentages of dry matter in the feces, not only for each 24-hour collection of feces during the fasting-periods, but likewise for the composite sample during the entire fast, are given in Table 21. Unfortunately, no daily analyses were made for the fasts in December 1921, November 1923, and February 1924. The data for the composite samples of feces during the feeding periods preceding and following the fasts are given in Table 22.

From these tables it can be seen that in general during the periods of maintenance feeding about 17 to 20 per cent of dry matter was present in the feces. During the periods of submaintenance feeding in February and March 1924 the percentage was not profoundly altered. The composite sample for the first fast in December 1921 likewise contained approximately 19.5 per cent of dry matter in the case of both steers. During the fasting experiments in January, April, and June 1922, there were considerable variations in the content of dry matter, with a distinct tendency, particularly in the 14-day fast, for the percentage of dry matter to decrease after the fourth to the sixth day. Up to this time, however, the percentage of dry matter is somewhat higher than during the prefasting feed period. In the fasts in November 1922 and March 1924, on the contrary, the percentage of dry matter increases considerably during the fast. It is difficult to account for these differences in the composition of the feces. The variations in the consumption of drinking-water seemingly explain the changes occasionally, but by no means give a satisfactory explanation for this anomalous situation. The matter is further complicated by reference to the notes made by the observers of the physical consistency of the feces at the time of passage. (See p. 89.)

In the two November fasts after pasture daily analyses were made only for the fast in 1922, but a composite sample was analyzed for the fast in 1923. For the fast following reduced rations in March 1924, daily samples were usually analyzed. In this fast and in that in November 1922 there is a distinct tendency for the percentage of dry matter in the feces of both steers to increase with the increasing length of the fast. The picture of the daily trend in the fast in November 1923 is not available, but the one analysis of the composite sample showed a percentage of dry matter of from 19.5 to 20 with both animals. Since, however, the feces on the first day of the fast in November 1922 had a very low content of dry matter, 16.5 and 16.7 per cent, respectively, and since the first day's defecation represents a large part of the total amount excreted during fasting, the low values found for the fast in November 1923 are what would be expected. The percentage of dry matter on the first day of the November 1922 fast, after the animals came in from pasture, is, however, very low as compared with that of the first day of the March 1924 fast, prior to which the animals had been subsisting upon a submaintenance ration of hay.

Table 22.—*Percentage of dry matter in composite samples of feces before and after fasts of 5 to 14 days*

Feed periods	Steer C	Steer D
Before fast:		
Nov. 26 to Dec. 6, 1921	18.4	27.7
Dec. 22 Jan. 4, 1922	19.2	19.4
Mar. 31 Apr. 17, 1922	19.4	20.7
May 9 June 1, 1922	17.6	17.4
Feb. 26 Mar. 3, 1924	23.0	21.9
After fast:		
Dec. 13 to Dec. 22, 1921	19.6	19.8
Jan. 14 Feb. 2, 1922	18.7	18.4
Mar. 21 Mar. 31, 1922	18.6	19.3
May 1 May 9, 1922	15.8	18.8
Mar. 12 Mar. 13, 1924	....	23.7
Mar. 13 Mar. 14, 1924	....	18.5
	Steer E	Steer F
Before fast:		
Jan. 28 to Feb. 12, 1924	21.9	21.1
After fast:		
Feb. 18 to Feb. 19, 1924	21.5	18.3
Feb. 19 Feb. 20, 1924	20.1	17.6

The difficulties of sampling feces and securing representative portions for analysis, the well-known loss during drying, and the general difficulty of securing anhydrous conditions in organic products make determinations of water in a substance such as the feces of ruminants at best somewhat uncertain. The extraordinarily high percentages of water noted in Table 21 in some of the feces, especially toward the end of the long fasts, has puzzled us greatly. Careful scrutiny of the raw data, checking of the computations, and a comparison with the ocular observations of the attending assistants confirm in large measure these low percentages of water-free matter. To explain them is not easy. It is evident that the finding of Grouven that the

TABLE 23.—*Daily weight of dry matter in feces before and during fasts of 5 to 14 days*

Steer and dates of fasts	Average on feed before fast[1]	Days fasting													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
	kg.	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*	*kg.*
Steer C:															
Jan. 4 to 14, 1922	4.15	3.49	1.72	0.86	0.37	0.43	0.41	0.39	0.18	0.10	0.13	......	......	......	......
Apr. 17 May 1, 1922	4.41	3.74	1.51	1.09	0.77	0.67	0.57	0.28	0.45	0.22	0.12	0.36	0.18	0.15	0.14
June 1 7, 1922	4.66	4.06	1.84	1.25	0.43	0.52	0.26	......	......	......	......	......	......	......	......
Nov. 6 16, 1922	....	2.21	1.32	0.74	0.62	0.35	0.24	0.24	0.49	0.31	......	......	......	......	......
Mar. 3 13, 1924	1.68	1.26	0.70	1.03	0.50	0.45	0.07	0.21	0.22	0.12	[2]0.00	......	......	......	......
Steer D:															
Jan. 4 to 14, 1922	3.82	3.26	2.10	0.66	0.49	0.49	0.30	0.35	0.24	0.16	0.13	......	......	......	......
Apr. 17 May 1, 1922	4.22	3.91	1.62	1.17	0.75	0.25	0.59	0.37	0.26	0.22	0.20	0.21	0.18	0.14	0.08
June 1 6, 1922	4.46	3.54	1.49	0.99	0.41	0.55	......	......	......	......	......	......	......	......	......
Nov. 6 14, 1922	....	2.26	1.13	1.04	0.30	0.63	0.23	0.52	0.07	......	......	......	......	......	......
Mar. 3 12, 1924	1.58	[3]1.16	[3]0.97	0.87	0.38	[4]0.60	[4]0.23	0.31	0.32	0.21	......	......	......	......	......

[1] Average daily dry matter for from 1 to 2 weeks on feed before fast. For exact dates represented, see Table 22, page 92.

[2] There were no defecations between 7 a. m., Mar. 12, and 7 a. m., Mar. 13, but 0.62 kg. feces were passed in the chamber between $7^h 10^m$ and $10^h 25^m$ a. m., Mar. 13, before the steer was fed. The dry matter in these feces was 20.6 p. ct. or 0.13 kg.

[3] Based on analysis of composite sample for Mar. 3 to 5.

[4] Based on analysis of composite sample for Mar. 7 to 9.

fill became more watery as the fast progressed may in part explain these feces with large percentages of water. Undoubtedly the feeding conditions prior to the fasts affected somewhat the composition of the feces, especially at the beginning of the fasts. In the latter part of the fasts, at the point when about 70 per cent of the dry matter of fill has been washed out through the feces, the moisture-content of the feces seems to be more rapidly affected by water intake in quantity above the physiological daily needs. It is conceivable that in the 14-day fasts the fill was rather liquid and contained a relatively small amount of dry matter of fibrous character. Hence there could not be much absorption of nutritive material, and consequently there was less absorption of water. Under these conditions the addition of water by drinking leaves the body partly in the feces, as there is less absorption. From the data it is clear that after the first 3 to 5 days the amount of dry matter defecated daily is more uniform than the total amount of feces, the greater variations corresponding in almost every instance to variations in the water intake. Further studies of the nature of the fill and feces voided during fasting, and particularly analyses of the fill in different parts of the alimentary tract at the end of long fasts, are imperative for a thorough understanding of the relationship between fill, water-content of fill, and excreted feces, as associated with the various stages of prolonged fasting.

It is perhaps more important to consider the actual amount of dry matter in feces as a measure of the loss of material to the animal during the fasting period. The weight of the dry matter in feces per day has, therefore, been recorded in Table 23 and in Fig. 4. Except for the fasts after submaintenance feeding, not far from 3.5 kg. of dry matter were excreted on the first day by the two large steers. This amount rapidly decreases to about 1 kg. on the third day, and to 0.5 kg. on the fifth day. Even on the last 4 days of the 14-day fast approximately 200 grams of dry matter were excreted on the average per day. In the fasts after submaintenance feeding the amount of dry matter on the first day was much smaller, being nearer 1.2 kg., but by the fifth day the excretion has become 0.5 kg., as in the other fasts. With the two small steers studied after submaintenance feeding, the dry matter was not determined for each day of the fast.

The analyses for steers C and D show that there is a continued loss of dry matter of ballast throughout the entire fast. In this respect the fecal excretion of the ruminant is strikingly different from that of the omnivorous man or dog, due without doubt to the large intestinal ballast.

Inasmuch as these animals were receiving no food, the total loss of dry matter during the various lengths of the fasts is important as giving an indication of at least the minimum amount of fill existing at the beginning of the experiment. For this purpose the total dry matter excreted in the feces by these animals has been recorded in Table 24, together with data regarding the daily amount of feed consumed during the week prior to the fast. In the longest fast of 14 days, about 10 kg. of dry matter were lost by both animals on a feed-level of 9 kg. of hay and 3 kg. of meal. If it is assumed that the dry matter in the feces of the steer represents on the average 20 per cent of the total fill, it can be seen that at the start of this 14-day fast the fill must have amounted to at least 50 kg. The evidence, however, is strikingly to the effect that the fill contains more than 80 per cent of water. The estimate of 50 kg., therefore, undoubtedly represents a minimum amount. Furthermore, it is clear that this estimate does not include all the fecal material, for some must have been retained.[a]

TABLE 24.—*Total weight of dry matter excreted in feces during fasts of 5 to 14 days*

Dates of fasts	Daily ration prior to fast		Steer C		Steer D	
	Hay	Meal	Days fasting	Total dry matter	Days fasting	Total dry matter
	kg.	*kg.*		*kg.*		*kg.*
Dec. 6 to 13, 1921	8.5	1.4	7	8.02	7	6.99
Jan. 4 14, 1922	7.0	6.0	10	8.08	10	8.18
Apr. 17 May 1, 1922	9.0	3.0	14	10.25	14	9.95
June 1 7, 1922	8.5	4.0	6	8.36	5	6.98
Nov. 6 16, 1922	Pasture		9	6.52	8	6.18
Nov. 4 10, 1923	Pasture		5	7.01	5	6.23
Mar. 3 13, 1924	4.5	....	10	4.56	9	5.05

In the 6-day fast in June 1922, steer C excreted 8.36 kg. of dry matter, or within 2 kg. of that excreted in 14 days. The ration prior to this fast contained 0.5 kg. less of hay and 1 kg. more of meal. After pasture, smaller amounts of dry matter were excreted and, as is to be expected, even in the 10-day fast following submaintenance feeding a total of but 4.5 and 5 kg. of dry matter were excreted by steers C and D, respectively. In this case the feed-level was 4.5 kg. of hay.

It is perhaps to be regretted that the animals were not slaughtered at the end of the fasting-periods, particularly at the end of the long fasts, in order to note the contents of the intestinal tract. Indeed, a study of the contents of the intestinal tract after various rations is imperatively needed, not only to give information regarding the physiological processes of digestion, but likewise regarding the proportion of fill to body-weight on varying rations.

NITROGEN IN FECES

The nitrogen excretion in the feces is of greatest significance in considering the nitrogen loss during fasting and in establishing a nitrogen balance, in which the nitrogen in the urine enters particularly into the calculation. It is important, however, to note also the rate of nitrogen loss in the fasting feces (presumably in large part in the form of undigested material) and the effect of the previous ration of hay and meal or of green grass. In Table 25, therefore, are recorded the average daily weights of nitrogen excreted in feces for the feed periods prior to the fast, and the total fecal nitrogen for

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[a] Colin (Traité de Physiologie Comparée des Animaux, 3d ed., Paris, 1888, 2, p. 693) found that a horse, which was slaughtered after having fasted for 30 days, had 26.2 kg. of fill in the intestinal tract. This finding emphasizes the necessity for bearing in mind in the study of these large ruminants that one has to deal continually with a possible ever-present source of energy. Although no analysis of the intestinal contents was reported by Colin, it is probable that the dry matter consisted for the most part not only of indigestible material, but of material not easily attacked by the normal intestinal flora of the horse.

TABLE 25.—*Daily nitrogen excretion in feces before and during fasts of 5 to 14 days*

Steer and dates of fasts	Average on feed before fast[1]	Days fasting														Total fecal nitrogen during fast
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Steer C:	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Jan. 4 to 14, 1922	80.0	65.1	26.2	14.5	6.6	8.1	6.2	6.5	3.5	2.9	3.1	.....	.....	.....	.....	142.7
Apr. 17 May 1, 1922	70.5	60.7	23.8	16.0	12.3	8.2	8.3	5.3	8.1	3.7	2.6	7.1	4.0	3.9	3.5	167.5
June 1 7, 1922	85.9	68.6	32.9	19.0	7.2	9.3	(2)	.....	.....	.....	.....	.....	.....	.....	.....	[2] 145.8
Nov. 6 16, 1922	....	47.2	27.9	15.6	13.6	7.7	6.4	6.1	11.2	7.1	.....	.....	.....	.....	.....	142.8
Mar. 3 13, 1924	26.3	20.3	11.3	16.1	6.6	6.5	1.1	4.8	3.9	2.3	.....	.....	.....	.....	.....	72.9
Steer D:																
Jan. 4 to 14, 1922	76.0	61.0	28.4	11.1	8.4	7.4	5.2	6.9	4.9	4.0	3.0	.....	.....	.....	.....	140.3
Apr. 17 May 1, 1922	64.4	63.6	22.4	16.4	12.7	4.8	9.3	6.1	5.1	4.6	3.9	4.3	3.7	3.0	2.2	162.1
June 1 6, 1922	84.5	61.7	27.5	20.8	7.1	10.2	.....	.....	.....	.....	.....	.....	.....	.....	.....	127.3
Nov. 6 14, 1922	....	47.0	23.1	21.6	6.5	14.3	4.7	14.3	1.6	.....	.....	.....	.....	.....	.....	133.1
Mar. 3 12, 1924	25.8	19.7	16.5	14.4	5.5	8.9	3.5	4.9	6.0	3.6	.....	.....	.....	.....	.....	83.0

[1] Average daily fecal nitrogen for from 1 to 2 weeks on feed before fast. For exact dates represented see Table 22, p. 92.

[2] No nitrogen analysis was made for the sixth day of this fast. The analysis of the composite sample for June 1 to 7 gave 0.292 p. ct. nitrogen in the fresh feces. On the basis of this analysis the total fecal nitrogen for 6 days would be 145.8 gm., and the fecal nitrogen on the sixth day would be 8.8 gm.

each day of the fasts. The daily weights of fecal nitrogen are also given in Fig. 4 for the fasts in April and November 1922 and March 1924. Special use of these data is made in considering the total nitrogen loss. (See p. 127.)

The only data available for comparison regarding the fecal excretion of large ruminants during fasting are those reported by Grouven in 1864.[a] The daily weights of feces and the contents of dry matter and nitrogen were determined by him in the case of a black ox which fasted for 8 days, a brown ox which fasted for 5 days, and ox I, which fasted for 4 days. The findings with steers C, D, E, and F completely confirm those of Grouven. Thus, Grouven noted that the daily weights of feces decreased as the fast progressed, the largest amounts occurring on the first day and some feces being excreted every day throughout the fast. Increasing percentages of dry matter and nitrogen were also noted by him in the case of the black and the brown oxen, but in the case of ox I there was practically no change in the percentage of nitrogen. The black and the brown oxen were slaughtered after their fasts, and it was found that the contents of the intestinal tract represented 10.7 per cent and 14.2 per cent, respectively, of the total live weight of the animal.

URINE

The urine is the path for the loss of considerable volumes of water and the chief outlet for metabolized nitrogen. Indeed, in nutrition experiments with steers, the nitrogen output in the urine has, for many years, been accepted as the best measure of protein metabolism. In connection with these fasting experiments, therefore, the amount, frequency, and regularity of urination was studied and an extensive chemical analysis was made of the constituents of the urine during fasting.

The collection of the urine for such studies requires special technique. With steers the technique is relatively simple, the essential requirements being the confinement of the animal in a stall and the use of a harness and a urine funnel, which is connected with previously weighed bottles in the basement beneath the stall. With cows the technique is more complicated. Not infrequently urine and feces are collected together, and since the urine contains metabolized nitrogen and the feces contain undigested nitrogen, the combined collection of urine and feces introduces an element of uncertainty into the determination of the nitrogen actually derived from body-tissue. During this research on fasting the steers wore urine funnels for months at a time, and doubtless some of the experiments represent the longest continuous periods in which stall feeding, metabolism experiments, and continuous collection of urine have been carried out.

In the collection of the urine during the fasting periods attention was given to the volume and the time of each individual urination, as well as to the total volume passed daily. Ordinarily the data regarding the amount of urine excreted are reported on the 24-hour basis. For a general study of the volume of urine, 24-hour collections of urine are perhaps sufficiently satisfactory. Since the steer will not voluntarily empty the bladder exactly at the end of each 24 hours, however, the apportionment of the urinations

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[a] Grouven, loc. cit., pp. 127 et seq.

during the 24-hour periods presents difficulty at times. Thus, if urine is passed a few minutes after 2 p. m., the beginning of the 24-hour period in most of our fasting experiments, it is a question whether this amount should be credited to the previous 24-hour period. Special discussion of this point will be given subsequently (see p. 110). In most instances the exact time of each voiding was recorded, so that it is possible to ascribe a certain urinary volume to a definite period of time since the last urination. These time records make possible a closer approximation to the true amounts of urine voided in any given time and are of special value in the more accurate chemical analysis of the urine and particularly in studying the influence of prolonged fasting and the differences between animals. Indeed, many of the data regarding the chemical constituents of the urine have been reported on the hourly basis (see Tables 28 and 29, pp. 108 to 111).

The physical properties of the urine, its color, odor, and density, were frequently determined. A study was also made during some of the later fasting periods of the reaction of each urination to litmus paper, in order to determine at what time in the course of the fast the normal alkaline urine of the steer becomes the acid urine of the carnivorous animal. The procedure was as follows: Twice daily the urine funnel and the urine hose were washed out with distilled water. At each urination several pieces of litmus

TABLE 26.—*Daily excretion of urine during 2-day fasts and three days with feed prior to fasts, steers C and D*

Steer and dates of fasts (1923)	Days before fast						Days fasting			
	3		2		1		1		2	
Steer C:	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Jan. 3 to 6...	4.92	15	5.34	12	5.47	11	2.67	6	[1] 3.30	9
Jan. 15 17...	5.16	25	4.88	20	5.86	26	4.27	29	3.06	12
Jan. 21 23...	2.83	28	3.92	27	6.54	29	3.74	28	2.88	7
Jan. 28 30...	3.32	11	4.87	26	6.19	11	5.28	8	2.20	25
Feb. 5 7...	5.56	12	5.16	4	4.71	7	4.81	6	2.80	5
Feb. 11 13...	3.18	8	4.08	10	5.42	11	5.16	8	3.20	8
Feb. 18 20...	4.16	− 3	5.20	3	4.90	7	4.86	4	3.50	0
Mar. 1 3...	5.18	12	6.06	13	5.38	11	5.06	12	3.42	14
Mar. 8 10...	3.18	4	4.68	3	4.84	4	4.04	4	2.17	6
Mar. 15 17...	4.18	10	4.08	7	3.90	5	4.58	8	2.77	8
Mar. 22 24...	3.68	19	4.36	24	4.40	27	4.18	26	2.70	22
Steer D:										
Jan. 9 to 12...	4.84	8	[2] 5.96	11	3.68	12	3.97	13	[1] 2.88	9
Jan. 17 19...	3.82	26	4.77	29	5.18	12	5.21	12	2.27	28
Jan. 25 27...	5.12	7	5.55	13	4.75	11	4.09	11	3.08	26
Feb. 1 3...	3.47	25	4.26	28	4.09	23	4.17	23	2.25	12
Feb. 8 10...	4.17	6	4.57	5	3.74	7	3.97	8	2.18	10
Feb. 14 16...	3.60	8	4.41	8	6.12	6	5.04	− 3	2.58	− 3
Feb. 22 24...	4.72	0	5.43	6	5.42	6	5.50	2	2.08	− 2
Mar. 5 7...	4.56	14	5.62	11	4.84	5	4.58	4	2.17	3
Mar. 13 15...	5.29	5	4.02	7	3.40	10	4.00	7	2.28	5
Mar. 20 22...	6.12	7	4.93	24	4.76	19	2.91	24	2.04	27

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[1] Steers C and D fasted a third day on Jan. 5–6 and Jan. 11–12, respectively; steer C voided 2.66 kg. of urine and steer D 5.16 kg.

[2] Steer went 24 hours without food preparatory to a proposed respiration experiment, but the experiment was not made.

paper were held under the end of the hose, enough urine always being left in the elbow of the hose after urination to wet the papers thoroughly. The hose was well drained after each litmus test. As a precaution against change in urine, the test should be made as soon as possible after the urine is passed.

INFLUENCE OF FASTING ON AMOUNTS OF URINE EXCRETED

AMOUNTS PER 24 HOURS AND PER HOUR

The amounts of urine excreted daily during the series of 2-day and 3-day fasts in 1923 and during 3 days just previous to each of these fasts are recorded in Table 26, together with the average stall temperature during the same 24 hours. It will be recalled that in the feeding-periods between these intermittent fasts the animals received a maintenance ration of 9 kg. of hay and 2 kg. of meal daily. The nutritive level was therefore held fairly constant. The most striking feature of this table is the distinctly lower amounts of urine excreted on the second day of fasting. On the first day occasional decreases in the 24-hour weights of urine are observed, but for the most part the amounts are essentially the same as those noted prior to the fasting periods.[a] The amount of urination, furthermore, is seemingly wholly independent of environmental temperature.

The interest centers chiefly, however, in the data for the fasts of 5 to 14 days' duration. The daily weights of urine during these fasts and for 3 days with feed before each of the fasts are given in Table 27. Since these fasts followed maintenance, submaintenance, or pasture feeding, and since steers E and F were much smaller and younger than steers C and D, variations in the urinary excretion are naturally to be expected. Finally, it must not be forgotten in the analysis of these data that the 24-hour weight of urine may actually represent a period much shorter or longer than 24 hours. Obviously, however, the more frequent the urination the greater the likelihood of the 24-hour collection representing the true 24-hour excretion.

In the three days prior to fasting, steer C excreted a maximum daily amount of 10.92 kg. of urine just preceding the fast in January 1922, and a minimum amount of 2.22 kg. prior to the fast following submaintenance feeding in March 1924. These extremes are not noted with steer D, the highest 24-hour amount excreted by him being 6.71 kg. prior to the fast in January 1922, and the lowest being 3.70 kg. prior to the March fast. In general, as is to be expected, the weights of urine during the 3 days on the submaintenance ration, that is, in March 1924, are considerably lower than those during the three days preceding the other fasts. Steers E and F prior to their fasts excreted small amounts, explainable on the two grounds that they were smaller animals and were on submaintenance rations.

During the actual fasting periods the maximum 24-hour excretion on the first day of the fasts following maintenance or pasture feeding was 13.03 kg., noted with steer D. The daily weights of urine have a tendency to decrease as the fast progresses. With steer C, minimum values are usually recorded on the fourth day, and the amounts stay reasonably constant from

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[a] The first day of fasting begins at 2 p. m., the last feed having been given between 7 and 8 a. m. of that day. The first feed following the fast was given during the last 3 hours of the last day of fasting (in two cases during the last 6 hours). This refeed usually induced a relatively liberal intake of water, which might have had an influence upon the volume of urine excreted.

there on, even when the fast extends to 14 days. With steer D the regularity is by no means so pronounced. In the first place, as large an amount as 13 kg. was found on the first day of the January fast. Secondly, a very high excretion of 7.65 kg. is noted on the tenth day of the fast in April 1922, and

TABLE 27.—*Daily excretion of urine before and during fasts of 5 to 14 days*

Steer and dates of fasts	Days before fast						Days fasting					
	3		2		1		1		2		3	
Steer C:	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Dec. 6 to 13, 1921	4.32	9	4.22	7	5.14	7	6.65	5	3.50	5	3.19	15
Jan. 4 14, 1922	6.51	16	6.73	16	10.92	14	9.41	20	4.46	20	3.35	20
Apr. 17 May 1, 1922	4.03	21	4.65	17	4.54	20	5.25	20	7.72	20	5.26	20
June 1 7, 1922	5.61	24	4.97	22	4.71	23	7.11	23	9.98	22	4.12	23
Nov. 6 16, 1922	....	....	....	....	....	....	6.02	....	3.57	....	1.83	....
Nov. 4 10, 1923	....	....	....	....	....	....	....	....	6.74	....	4.31	....
Mar. 3 13, 1924	2.74	13	2.22	16	3.74	17	[1] 1.91	14	2.18	16	1.23	16
Steer D:												
Dec. 6 13, 1921	4.42	9	4.12	7	5.08	7	8.59	5	2.96	5	1.49	15
Jan. 4 14, 1922	6.71	16	6.30	16	6.38	14	13.03	20	3.60	20	4.03	20
Apr. 17 May 1, 1922	4.88	21	4.75	17	5.50	20	5.71	20	6.73	20	6.98	20
June 1 6, 1922	5.78	24	4.73	22	5.52	23	6.91	23	4.05	22	8.91	23
Nov. 6 14, 1922	....	....	....	....	....	....	6.30	....	2.93	....	2.82	....
Nov. 4 9, 1923	....	....	....	....	....	....	....	....	9.17	....	3.56	....
Mar. 3 12, 1924	3.70	13	3.90	16	4.03	17	[1] 3.20	14	4.82	16	1.40	16
Steer E:												
Feb. 12 17, 1924	1.76	12	2.04	12	1.93	13	1.34	16	5.00	15	1.14	16
Steer F:												
Feb. 12 18, 1924	1.37	12	1.72	12	1.70	13	1.40	16	1.21	15	0.91	16

Steer and dates of fasts	Days fasting											
	4		5		6		7		8		9	
Steer C:	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Dec. 6 to 13, 1921	1.97	20	2.98	18	2.67	17	1.67	20	....	....	....	....
Jan. 4 14, 1922	1.68	21	2.36	24	4.64	20	2.13	20	1.67	21	1.60	23
Apr. 17 May 1, 1922	3.16	15	2.03	20	3.84	22	2.18	22	1.92	22	2.09	23
June 1 7, 1922	2.55	25	3.09	27	2.40	26	....	....	....	....	....	....
Nov. 6 16, 1922	2.99	....	2.88	....	1.93	....	2.68	....	2.66	....	2.67	....
Nov. 4 10, 1923	2.70	....	2.91	....	3.32	....	....	....	....	....	....	....
Mar. 3 13, 1924	2.54	16	0.65	14	0.94	16	2.23	18	1.73	14	1.64	16
Steer D:												
Dec. 6 to 13, 1921	5.55	20	1.83	18	1.47	17	5.02	20	....	....	....	....
Jan. 4 14, 1922	3.19	21	3.19	24	3.07	20	4.33	20	1.89	21	1.36	23
Apr. 17 to May 1, 1922	3.20	15	2.43	20	2.29	22	1.57	22	1.87	22	1.92	23
June 1 6, 1922	3.01	25	7.40	27	....	....	....	....	....	....	....	....
Nov. 6 14, 1922	3.31	....	5.72	....	3.94	....	2.11	....	2.02	....	....	....
Nov. 4 9, 1923	3.23	....	2.66	....	....	....	....	....	....	....	....	....
Mar. 3 12, 1924	3.25	16	3.15	14	1.74	16	3.35	18	2.50	14	1.25	16
Steer E:												
Feb. 12 to 17, 1924	5.27	15	....	....	....	....	....	....	....	....	....	....
Steer F:												
Feb. 12 to 18, 1924	1.09	15	1.23	14	....	....	....	....	....	....	....	....

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[1] This value represents a period of only 17 hours, from 2 p. m. to 7 a. m.

TABLE 27.—*Daily excretion of urine before and during fasts of 5 to 14 days*—Continued

Steer and dates of fasts	Days fasting									
	10		11		12		13		14	
Steer C:	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*	*kg.*	° *C.*
Jan. 4 to 14, 1922	1.86	23	....	....	....	....	....	....	....	....
Apr. 17 May 1, 1922	2.12	20	4.63	22	2.01	21	1.61	21	2.35	21
Mar. 3 13, 1924	2.23	16	....	....	....	....	....	....	....	....
Steer D:										
Jan. 4 14, 1922	2.47	23	....	....	....	....	....	....	....	....
Apr. 17 May 1, 1922	7.65	20	2.32	22	3.81	21	5.68	21	1.90	21

an extremely low amount of 1.49 kg. on the third day of the fast in December 1921. This animal is characterized, therefore, by a much greater irregularity in the excretion of urine. In the fasts following pasture, when the body was full of a succulent feed, the results are not strikingly different from those noted in the fasts following maintenance feeding. But in the fasts following submaintenance feeding in March 1924 a much lower level of excretion was noted throughout practically the entire fasting period with both animals. This finding is in full conformity with the decreased volumes observed prior to this fast.

The hourly excretion of urine has likewise been computed for these fasts of 5 to 14 days, and the data have been recorded in Tables 28 and 29 (pp. 108 to 111), from which it can be seen that the volume of urine excreted per hour during fasting undergoes enormous changes. The largest hourly excretion was noted with both steers on the same date, January 4–5, 1922, being 384 c. c. in the case of steer C and 535 c. c. in the case of steer D. The lowest values occur, as perhaps is to be expected, during the fasts in March 1924, following submaintenance feeding, when the hourly excretion of steer C was as low as 52 c. c. on March 12–13, and that of steer D was as low as 46 c. c. on March 5–6. With steers E and F in their fasts following submaintenance rations the hourly values likewise vary considerably. A careful analysis of this decrease is possible only when the amounts of drinking-water consumed are taken into consideration. In general, when the steer is on submaintenance rations, the water intake is smaller and the volume of urine is naturally considerably smaller.

THE FREQUENCY AND AMOUNT OF INDIVIDUAL URINATIONS DURING FASTING

A study of the influence of fasting and the amount of drinking-water upon the frequency of urination and the volume of each individual urination was possible in all of the fasts of 5 to 14 days. The 14-day fast in April 1922, after maintenance feeding, the fast after pasture feeding in November 1922, and the fast following submaintenance feeding in March 1924, have been selected as illustrations for this study. These three represent typical fasts under the varying feed conditions, the fast in April following maintenance rations being typical of the larger number of the fasts. The pertinent data have been charted in Fig. 7. The curves show graphically the times of urination and the actual amounts involved. The figures in the upper row above each curve represent the total weights of drinking-water during the 24-hour periods and the figures in the lower row the total weights of urine.

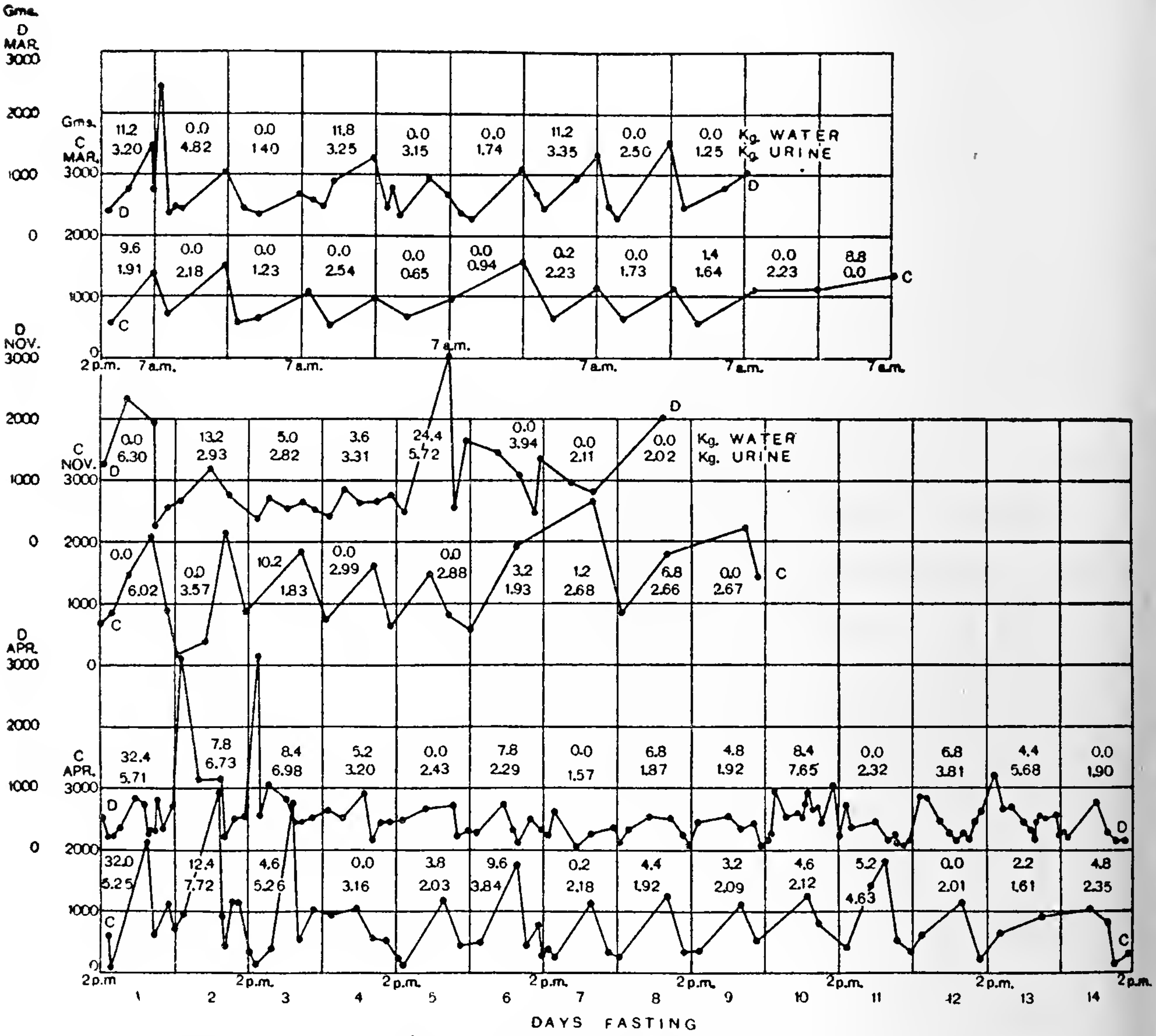

FIG. 7.—Individual urinations of steers C and D during fasts in April and November 1922 and March 1924

The two curves at the bottom of the chart represent the fasts in April 1922, which followed maintenance feeding. Those in the center are for the fasts in November 1922, following pasture feeding, and the two at the top are for the fasts in March 1924, following submaintenance feeding. The figures in the upper row above each curve represent the amounts of drinking-water (in kilograms) taken in every case at the beginning of the 24-hour period. The figures in the lower row represent the total kilograms of urine voided during the 24-hour periods.

The frequency of urination varied considerably with steers C and D. In general, steer D urinated more frequently throughout the day than did steer C, and the total volumes were somewhat different. Thus, the total amount of urine excreted by steer C in the 14-day fast was 46.17 kg. and by steer D was 54.06 kg. On those days when peaks in the curve occur, showing large volumes of urine, one finds a correlation with water intake only rarely. Thus, in the March fast, at the beginning of the seventh day, when steer D drank 11.2 kg. of water, there was but a small increase in the 24-hour amount of urine excreted. On the two following days, when he drank no water, the total amount of urine decreased, to be sure, but not at all in proportion to the decrease in the water intake. On the other hand, with steer D, on the fifth day of the fast in November 1922, after pasture, an intake of water of 24.4 kg. is followed by a very large urination. On the whole, however, there is no distinct evidence of a pronounced relationship between water intake and volume of urine.

The maximum individual urinations occurred with steer D. In the fast following pasture 3,048 grams were voided on the fifth day and on the second and third days of the April fast 3,122 and 3,151 grams, respectively, were voided. Very small amounts were also frequently passed by steer D. Thus, as early as on the seventh day of the April fast, an amount less than 100 grams was passed, and on three subsequent days in this same fast amounts under 100 grams were also passed. With steer C on the first day of the April fast a small voiding of 99 grams occurred. Large changes in the content of the bladder needed to stimulate voiding thus seem possible, even under these restricted conditions. A possible explanation of the variability in the individual urinations might be the temperature to which the animals were exposed. (See the records of stall temperatures in Table 27, p. 100.) A careful examination of the records, however, shows no correlation between the two factors. Usually both animals were essentially at the same temperature, not far from 15° to 20° C., the entire time. A study of the influence of environmental temperature upon the urinary volume would be more significant, if made on days when the steer was receiving a constant ration, prior to any fasting. Our evidence is not complete for this purpose, but, so far as it goes, there is nothing to indicate any relationship between the environmental temperature and the weight of urine.

Relation Between Volume and Dry Matter of Urine

The necessity for the addition of a preservative to the urines of these steers and the length of time that the urines had to be stored made late determinations of the specific gravity or total solids unsatisfactory, and hence our evidence on the relation between the volume and the dry matter of urine is somewhat uncertain. From our observations in the research on undernutrition in steers it was clear that the volumes of urine, as was the case with the urines of these fasting steers, were not profoundly affected by variations in the amount of nitrogen in the urine, and surprisingly little affected by relatively large changes in the amount of drinking-water consumed.

Physical Properties of the Urine

In general, during normal feeding, such as usually preceded a fast, the urine was of a dilute yellowish-brown color, tending towards opaqueness in proportion to the relative daily amount voided. Thus, when the amount was extraordinarily large, the urine, because diluted, was lighter colored than when the amount was unusually small and concentrated. As the fast progressed and less water was consumed by the animal, the volume of urine usually decreased and the color became darker, very small volumes often being almost black in appearance. The darker the color of the urine the more intense and offensive became the odor, probably because the urine was voided at longer intervals and the decomposition in the bladder was further advanced before the urine was voided. (See p. 121.)

CHEMISTRY OF THE URINE

The chemical analysis of the urine, particularly with reference to the various nitrogenous ingredients and the apportionment of the total nitrogen among the various compounds, has proved of great physiological interest and of inestimable chemical value in the case of humans. The possibility of studying the urinary output of a large ruminant during fasting and comparing the results with analyses of the characteristically different urines prior to fasting made such a study an important part of our program. Dr. Thorne M. Carpenter, of the Nutrition Laboratory, has undertaken the analysis of such samples of urine as could be secured from our fasting steers, and the following discussion is for the most part based upon a detailed report which he is soon to publish. Preliminary communications on this subject have already been made by Dr. Carpenter.[a]

URINE ANALYSES BY OTHER INVESTIGATORS

The many characteristics of the urine of herbivora obviously different from the characteristics of human urine, such as the high alkaline reaction, the presence of carbonates, and differences in color and odor, would naturally suggest that the urine of herbivora is a physiological fluid of vastly different chemical nature from that excreted by humans. That this problem has already interested research workers is evidenced by the fact that as far back as 1864 Grouven[b] devoted not a little attention to the subject, but unfortunately with very defective methods. Indeed, Grouven was the first to collect and analyze the urines of fasting steers. The weight, specific gravity, total nitrogen, dry matter, and ash were determined. In a few instances the hippuric acid was estimated. Five animals were studied in 9 fasts which varied from 43½ hours to 8 days in length. All of the fasts were preceded by feeding periods of from 3 to 14 days, the ration usually being circa. 3.5 kg. of rye straw. In an 8-day fast of an ox weighing 522 kg. the nitrogen elimination on the first two days was 32 gm. per day, on the third and fourth days 54 gm., on the fifth and sixth days 40 gm., and on the seventh and eighth days 68 gm. In a 5-day fast with an ox weighing 420 kg. the nitrogen elimination was 42 gm. per day on the first two days, 54 gm. on the next two days, and 51 gm. on the last day. With an animal weighing 535 kg. the nitrogen excretion varied from 20 gm. on the first day of fasting to 50 gm. on the fourth day. The other fasts were of 3 days' duration or less. In several of them the nitrogen excretion was extremely low, the lowest amount being 17 gm. on the first day.

The subject then remained almost entirely unstudied until 1906, when Baer reported the effect of the withdrawal of carbohydrate upon various animals, with reference to the onset of acidosis. Among the animals used

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[a] Carpenter, Journ. Biol. Chem., 1923, 55, p. iii; ibid., Proc. Nat. Acad. Sci., 1925, 11, p. 155.

[b] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salmünde, Berlin, 1864, pp. 127 to 195.

were 3 goats which fasted for a period of 3 days and then were given phlorizin. The details of this study must be secured from the original report.[a] Of special interest is the 24-hour urinary nitrogen per kilogram of body-weight, which calculation shows to be 0.28 and 0.29 gm. on the first fasting day, i. e., a nitrogen-level considerably higher than that found with our fasting steers. The ammonia constituted a small proportion of the total nitrogen-content, with but little evidence of an acidosis. The excretion of acetone was small and remained essentially constant during the fast.

Prayon,[b] in 1910, studied the creatinine excretion in the urines of an ox, a bull, and a mare during periods of normal feeding and during a 3-day fasting period. He determined only the percentage content of creatinine, however, and computed the weight of the creatinine from an assumed volume of urine per day.

In 1920, Blatherwick,[c] studying the regulation of neutrality in the blood of cattle, made determinations on the plasma and urine of a cow which fasted and practically went without water for 7 days. The results of the urine analyses are reported per 100 c. c. of urine. The ammonia increased from 7 to 13 mg. in 4 days and the phosphorus from 20.6 to 156.3 mg. in 7 days. The author concludes that the only evidence of acidosis is the fact that the phosphorus in the blood plasma showed an increase in the early part of the fast.

In this same year Peters[d] published the results of his study of the urines of normal goats upon different diets, fasting, and after feeding with acid and alkali, with special reference to the acidity reaction, the titratable alkalinity, the hydrogen-ion concentration, and the excretion of ammonia and chlorides. Two goats fasted for 24 hours and one goat fasted for 48 hours. The urines became more acid as the result of fasting, and in each instance reached the greatest acidity on the day following the fasting period. The ammonia excretion on the first day of fasting was 0.032 gm. per 24 hours with a goat weighing 26 kg. and 0.072 gm. with a goat weighing 24 kg. The lighter weight goat also fasted a second day, when the ammonia excretion was 0.105 gm.

Two communications were made by Palladin[e] in 1924, who studied particularly the creatine and the creatinine in the urine of adult sheep fasting for various lengths of time. A sheep weighing 88 kg. had lost 12 kg. after a 9-day fast. At the beginning of the fast the total nitrogen in the urine amounted to 11.26 gm. for 24 hours, and at the end of the fast to 5.4 gm. Creatinine was excreted during the entire fast, as was creatine after the first day. The urinary nitrogen per kilogram of body-weight per 24 hours was 0.128 gm. on the first day of the fast and 0.071 gm. on the last day. The creatinine coefficient was 19.0 mg. on the first day and 18.1 mg. on the

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[a] Baer, Arch. f. exp. Path. u. Pharm., 1906, **54**, p. 153.

[b] Prayon, Methoden zur Bestimmung des Kreatinins im Harne und Untersuchungen über Kreatininausscheidungen im Harne der Herbivoren. Inaug.-Diss., Bern, 1910.

[c] Blatherwick, Journ. Biol. Chem., 1920, **42**, p. 517.

[d] Peters, Biochem. Journ., 1920, **14**, p. 697.

[e] Palladin, Arch. f. d. ges. Physiol., 1924, **203**, p. 93; ibid., **204**, p. 150.

last day. A second sheep, weighing 58.4 kg., fasted 16 days and lost 13.6 kg. The total urinary nitrogen on the first day was 19.05 gm. and on the last day 6.17 gm. Creatinine was excreted during the entire fast. Creatine began to be excreted on the third day and the excretion continued throughout the fast. The nitrogen excreted per kilogram of body-weight per 24 hours was 0.326 gm. at the beginning and 0.138 gm. at the end. The creatinine coefficient fell from 20.0 to 15.5 mg. In a second communication the results are given for an adult sheep, which weighed 64 kg. and fasted 8 days. The nitrogen in the urine on the first day was 9.43 gm., on the second day 10.42 gm., and on the eighth day 5.40 gm. per 24 hours. The author believes that during fasting there is an increase in the formation of acids and that in the neutralization of these acids the excretion of ammonia is increased. A comparison of the effect of an acid feed, such as oats, with an alkaline feed following the fast showed a greater ammonia excretion with the acid feed.

In connection with a study of the metabolism in acetonemia, Sjollema and van der Zande[a] determined the total acetone bodies, ammonia nitrogen, phosphoric acid, glucose, and calcium in the urine of milch cows. On three different occasions they attempted to provoke acetonemia experimentally by producing glycosuria with injections of phlorizin followed by fasting. They found that during the days of the injections the urine contained 2.2 to 2.4 per cent of glucose, but no acetone bodies. Ketonuria occurred only when, after some days of phlorizin glycosuria, no food was given to the cows for 2 days. The quantity of acetone, however, was much lower than in typical acetonemia, about 0.4 gm. in 1,000 c. c. They conclude, therefore, that the cow does not easily produce much acetone, except in certain diseased conditions.

The most recent contribution to this study of the urine of fasting ruminants is that of Forbes, Fries, and Kriss,[b] who, following a plan of Professor Armsby, studied cows which fasted for 3, 6, and 9 days. Since the urine and feces were not separated as a rule, it was possible to study the urine on only a few days. During a 10-hour period at the end of the fourth fasting day one cow voided 1.518 kg. of urine containing 28 gm. of nitrogen. During the succeeding 24 hours she passed 1.804 kg. of urine containing 26.5 gm. of nitrogen. Another cow on the sixth fasting day voided in 24 hours 1.978 kg. of urine with a nitrogen content of 28.2 gm. At the end of 7½ days she excreted 42.8 gm. of nitrogen in a 24-hour period. In the case of another cow on the sixth day 21.1 gm. of nitrogen were excreted in 24 hours. The daily nitrogen excretion of this same cow during the sixth to the ninth day of fasting was 28.7 gm. and during the seventh to the ninth day was 31.2 gm. The difficulty of separating the urine and feces of cows has for years retarded the study of the urine *per se* with cows. A satisfactorily functioning mechanical device (eliminating the use of a harness or other encumbrances) for the separation of the urine and feces of cows has been developed at the New Hampshire Agricultural Experiment Station by one of us (E. G. R.) and at the moment of writing is being most successfully employed.

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[a] Sjollema and van der Zande, Journ. Metabolic Research, 1923, **4**, p. 525.

[b] Forbes, Fries, and Kriss, Journ. Dairy Sci., 1926, **9**, p. 15.

CHEMICAL METHODS

Preservation of urine—The necessity of transporting the urines from Durham to Boston, the unavoidable delay in the analyses at the Nutrition Laboratory, and the lack of refrigeration made it imperative to develop a method for the preservation of the urines. Willinger[a] reports that the urine of 12 large ruminants had an average p_H of 8.70. Since this would predispose towards spoiling, we took immediate steps to have the urine made acid. Varying amounts of concentrated hydrochloric acid were placed in the collection bottles, and if, in spite of this, it was found at the time of weighing the bottles and contents that the urine was still alkaline, further acid was added until the urine reacted acid. We have evidence that decomposition of some nitrogenous substances takes place rapidly in the original urine, even in the presence of thymol or chloroform. Undoubtedly creatinine rapidly disappears.

Methods of analysis—To the collected volume of urine there was automatically added a certain amount of water whenever the collection was made inside the respiration chamber, this water being necessary to seal the trap in the urine hose. The analyses were made on the volumes of urines, and consequently it was necessary to calculate the volume of the urine plus the water and hydrochloric acid added. The analyses of the nitrogenous constituents were for the most part made by the commonly accepted superior methods of Folin and his associates,[b] but in the case of the phenols, for example, Tisdall's modification of Folin's method was used.[c]

STATISTICS OF RESULTS

It is impossible to report in detail in this monograph the results of all the innumerable analyses carried out by Dr. Carpenter and his associates, and reference must be made for such details to the extensive discussion of the urines of these fasting steers to be published later. In the fasts of steers C and D up to and including those in November 1922, the chief urinary constituents determined were the total nitrogen and the total chlorides. The data for these determinations, together with the records of the volumes of urine excreted, have been summarized in Table 28. In the fasts of steers C and D in November 1923 and March 1924, and in the fasts of the two younger steers, E and F, in February 1924, much more extensive urine analyses were carried out. The study of the total nitrogen has long been considered an important one, but this study has now been surpassed, thanks to the researches of Folin, by an interest in the partition of the nitrogen. The analyses of the urines during these later fasts therefore included the partition of the nitrogen according to modern methods, and the results have been recorded in Table 29. Since it was necessary to preserve the urines in these later fasts with hydrochloric acid, no determinations of the chlorides were made, but determinations were made of the total nitrogen, urea-nitrogen, ammonia-nitrogen, amino-acid nitrogen, hippuric-acid nitrogen, and preformed and total creatinine, the data for all of which are given in

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[a] Willinger, Arch. f. d. ges. Physiol., 1924, **202**, p. 468.

[b] Folin, Laboratory manual of biological chemistry, New York, 1922.

[c] Tisdall, Journ. Biol. Chem., 1920, **44**, p. 409.

TABLE 28.—*Volume of urine and total nitrogen and chlorides in urines of steers C and D from December 1921 through November 1922*

Date and steer	Duration of period	Volume of urine		Total nitrogen		Chlorides (NaCl)	
		Total	Per hour	For period	Per hour	For period	Per hour
1921	*hrs.*	*liters*	*c. c.*	*gm.*	*gm.*	*gm.*	*gm.*
Steer C:							
Nov. 26 to Dec. 6	10 days	[1]45.74	[2]191	594	2.48	....	....
Dec. 6– 7	24	6.46	269	64.7	2.70	29.0	1.21
Dec. 7– 8	22	3.40	157	60.0	2.77	5.56	.257
Dec. 8– 9	26	3.10	117	81.5	3.08	1.82	.069
Dec. 9–10	18	1.91	103	42.3	2.29	1.06	.057
Dec. 10–11	24	2.91	122	50.8	2.13	1.42	.060
Dec. 11–12	28	2.60	93	55.5	1.98	1.46	.052
Dec. 12–13	18	1.62	91	42.7	2.41	.823	.046
Dec. 13 to Dec. 22	9 days	[1]32.28	[2]149	280	1.30	....	....
Steer D:							
Nov. 26 to Dec. 6	10 days	[1]44.17	[2]184	575	2.40	....	....
Dec. 6– 7	24	8.43	351	49.3	2.05	34.0	1.42
Dec. 7– 8	24	2.87	121	50.7	2.13	8.77	.369
Dec. 8– 9	24	1.42	60	48.3	2.03	.290	.012
Dec. 9–10	25	5.46	223	61.2	2.50	....	....
Dec. 10–11	[3]16	[3]1.79	112	[3]32.7	2.05	....	....
Dec. 11–12	25	1.40	57	53.1	2.14	.305	.012
Dec. 12–13	25	4.94	200	50.7	2.06	.820	.033
Dec. 13 to Dec. 22	9 days	[1]33.99	[2]157	210	.97	....	....
Steer C:							
Dec. 22, 1921, to Jan. 4, 1922	13 days	[1]67.46	[2]216	1242	3.98	....	....
1922							
Jan. 4– 5	24	9.21	384	123	5.15	42.9	1.79
Jan. 5– 6	24	4.30	179	118	4.91	10.5	.438
Jan. 6– 7	24	3.21	134	89.8	3.74	2.58	.108
Jan. 7– 8	16	1.62	103	44.2	2.81	.727	.046
Jan. 8– 9	29	2.25	78	66.9	2.31	1.67	.058
Jan. 9–10	28	4.54	165	62.3	2.27	4.60	.167
Jan. 10–11	21	2.07	98	37.1	1.77	3.39	.162
Jan. 11–12	27	1.60	59	43.6	1.61	.900	.033
Jan. 12–13	18	1.55	86	30.4	1.68	1.75	.097
Jan. 13–14	27	1.80	67	44.7	1.66	2.28	.084
Jan. 14 to Feb. 2	18 days	[1]66.61	[2]154	802	1.86	....	....
Steer D:							
Dec. 22, 1921, to Jan. 4, 1922	13 days	[1]67.75	[2]217	1320	4.23	....	....
Jan. 4– 5	24	12.84	535	122	5.07	48.7	2.03
Jan. 5– 6	23	3.46	150	89.9	3.91	16.7	.728
Jan. 6– 7	26	4.42	173	85.4	3.35	4.26	.167
Jan. 7– 8	24	3.10	129	66.8	2.78	....	....
Jan. 8– 9	23	3.11	138	57.0	2.53	....	....
Jan. 9–10	22	3.00	139	49.9	2.32	....	....
Jan. 10–11	28	4.25	152	55.7	1.99	....	....
Jan. 11–12	23	1.83	80	37.8	1.64	....	....
Jan. 12–13	22	1.32	61	32.2	1.50	....	....
Jan. 13–14	26	2.43	93	35.6	1.37	1.17	.045
Jan. 14 to Feb. 2	19 days	[1]75.12	[2]165	905	1.99	....	....

[1] Kilograms. [2] Grams. [3] Urine for the period 2 p. m. to 7^{h}31^{m} p. m. Dec. 10 was lost.

TABLE 28.—*Volume of urine and total nitrogen and chlorides in urines of steers C and D from December 1921 through November 1922*—Continued

Date and steer	Duration of period	Volume of urine		Total nitrogen		Chlorides (NaCl)	
		Total	Per hour	For period	Per hour	For period	Per hour
1922	*hrs.*	*liters*	*c. c.*	*gm.*	*gm.*	*gm.*	*gm.*
Steer C:							
Mar. 31 to Apr. 17	17 days	[1]68.11	[2]167	1229	3.01	....	....
Apr. 17–18	24	5.18	216	78.2	3.26	55.4	2.31
Apr. 18–19	21	7.63	363	75.2	3.58	13.7	.655
Apr. 19–20	24	5.21	217	67.8	2.83	....	....
Apr. 20–21	24	3.10	129	78.6	3.28	....	....
Apr. 21–22	24	1.97	82	57.9	2.41	1.72	.072
Apr. 22–23	27	3.78	140	63.9	2.37	1.19	.044
Apr. 23–24	21	2.13	101	42.9	2.03	.926	.044
Apr. 24–25	24	1.87	77	48.8	2.00	.972	.040
Apr. 25–26	24	2.03	86	52.3	2.23	.563	.024
Apr. 26–27	21	2.07	101	34.3	1.67	1.06	.052
Apr. 27–28	30	4.57	151	51.9	1.71	5.42	.179
Apr. 28–29	22	1.97	90	36.3	1.65	2.01	.092
Apr. 29–30	20	1.57	78	39.7	1.99	1.45	.073
Apr. 30–May 1	30	2.31	77	47.2	1.57	2.61	.087
May 1 to May 9	8 days	[1]19.30	[2]101	222	1.16	....	....
Steer D:							
Mar. 31 to Apr. 17	17 days	[1]74.95	[2]184	1304	3.20	....	....
Apr. 17–18	24	5.54	231	91.1	3.80	53.6	2.23
Apr. 18–19	24	6.64	273	88.9	3.65	19.0	.779
Apr. 19–20	22	6.94	322	78.7	3.65	7.52	.349
Apr. 20–21	25	3.14	124	71.1	2.80	.927	.037
Apr. 21–22	25	2.38	97	62.3	2.53	1.47	.060
Apr. 22–23	24	2.23	92	56.5	2.33	1.48	.061
Apr. 23–24	24	1.54	65	38.9	1.66	.621	.026
Apr. 24–25	25	1.82	74	44.0	1.80	....	....
Apr. 25–26	24	1.89	80	38.3	1.63	....	....
Apr. 26–27	25	7.63	305	45.1	1.80	6.90	.276
Apr. 27–28	24	2.28	96	35.0	1.48	4.65	.196
Apr. 28–29	24	3.76	155	37.3	1.54	6.67	.275
Apr. 29–30	23	5.63	242	35.8	1.54	7.11	.305
Apr. 30–May 1	22	1.87	85	33.9	1.54	2.12	.096
May 1 to May 9	8 days	[1]22.40	[2]117	208	1.08	....	....
Steer C:							
May 9 to June 1	23 days	[1]103.39	[2]187	1839	3.33	572	1.04
June 1– 2	24	6.91	288	100	4.19	39.3	1.64
June 2– 3	24	9.76	407	103	4.30	50.3	2.10
June 3– 4	23	4.00	176	80.5	3.57	11.1	.492
June 4– 5	23	2.45	105	62.0	2.67	3.09	.133
June 5– 6	24	2.98	125	60.8	2.54	4.00	.167

[1] Kilograms.

[2] Grams.

TABLE 28.—*Volume of urine and total nitrogen and chlorides in urines of steers C and D from December 1921 through November 1922*—Continued

Date and steer	Duration of period	Volume of urine		Total nitrogen		Chlorides (NaCl)	
		Total	Per hour	For period	Per hour	For period	Per hour
1922	*hrs.*	*liters*	*c. c.*	*gm.*	*gm.*	*gm.*	*gm.*
Steer D:							
May 9 to June 1......	23 days	[1]101.22	[2]183	1902	3.45	599	1.09
June 1– 2..........	23	6.70	291	93.8	4.08	73.1	3.18
June 2– 3..........	24	3.90	159	96.2	3.93		
June 3– 4..........	24	8.78	363	88.1	3.64		
June 4– 5..........	24	2.90	122	66.1	2.77	1.87	.078
June 5– 6..........	23	7.28	317	62.9	2.73		
Steer C:							
Nov. 6– 7..........	22	[3]5.79	[3]263	[3]99.0	[3]4.50		
Nov. 7– 8..........	26	3.42	133	100.6	3.92		
Nov. 8– 9..........	18	1.76	99	59.4	3.35		
Nov. 9–10..........	30	2.88	97	94.5	3.19		
Nov. 10–11..........	25	2.79	112	80.0	3.21		
Nov. 11–12..........	16	1.86	119	49.3	3.16		
Nov. 12–13..........	25	2.57	104	73.4	2.97		
Nov. 13–14..........	24	2.55	105	66.5	2.74		
Nov. 14–15..........	29	2.58	89	72.0	2.48		
Steer D:							
Nov. 6– 7..........	22	6.06	276	99.4	4.52		
Nov. 7– 8..........	20	2.82	139	91.6	4.51		
Nov. 8– 9..........	28	2.72	97	93.3	3.34		
Nov. 9–10..........	25	3.21	127	80.0	3.18		
Nov. 10–11..........	24	5.58	237	86.0	3.65		
Nov. 11–12..........	25	3.84	155	71.3	2.88		
Nov. 12–13..........	17	[4]1.84	[4]109	[4]47.8	[4]2.84		
Nov. 13–14..........	24	1.94	81	54.5	2.28		

[1] Kilogram. [2] Grams. [3] Some urine was spilled.

[4] Approximately 200 grams of urine were lost.

Table 29. In practically all of the fasts other urinary constituents were also determined, such as inorganic sulphate, ethereal sulphate, neutral sulphur, and total sulphur, the free and conjugated phenols, acetone and diacetic acid (determined together), β-oxybutyric acid, total fixed bases, and the organic acids, but reference must be made to Carpenter's report for these details.

The ever-present complexity of irregularity in the voiding of urine and the high probability of the incomplete emptying of the bladder, particularly at the end of the period of collection, make the study of the urinary output and its constituents on any time basis always somewhat approximate. Because of the inability to secure sharply divided 24-hour periods, the record of the exact time of each urination became important, and this was usually noted carefully in the later fasts. In the earlier fasts the lack of enough assistants made such records somewhat uncertain, although they were kept. In general, however, each period of collection represents not far from a 24-hour day. In the fasts recorded in Table 28 the periods of collection have been recorded to the nearest hour, as they were all approxi-

Date and steer	Duration of period		Volume of urine	Total nitrogen	Urea-nitrogen	Ammonia-nitrogen	Amino-acid nitrogen	Hippuric-acid nitrogen	Preformed creatinine	Total creatinine
1923										
Steer C:	*hrs.*	*min.*	*c. c.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Nov. 5– 6	24	....	275	3.63	2.75		0.038	0.134	0.52	0.79
Nov. 6– 7	22	....	191	4.32	3.36		.021	.097	.60	1.07
Nov. 7– 8	24	....	110	3.24	2.68		.014	.047	.57	.97
Nov. 8– 9	24	....	119	2.65	2.15		.010	.035	.59	.75
Nov. 9–10	23	....	144	2.45	1.82		.015	.036	.61	.71
Steer D:										
Nov. 5– 6	24	....	323	3.38	2.66		.067	.114	.53	.76
Nov. 6– 7	24	....	145	3.82	3.14		.013	.075	.74	1.06
Nov. 7– 8	22	....	146	3.71	2.44		.016	.059	.74	1.09
Nov. 8– 9	26	....	100	2.81	2.08		.009	.036	.66	.78
Nov. 9–10	24	....	71	2.02	1.51		.007	.037	.43	.53
1924										
Steer C:										
Feb. 27–29 and Mar. 1– 2	3 days		107	.67	....	....	....	....	....	....
Mar. 2– 3	22	8	161	1.49	....	....	.265	.409	.72	.80
Mar. 3	4	17	121	.99	0.26	0.067	.059	....	.61	.63
Mar. 3– 4	14	26	92	.79	.32	.017	.024	.071	.54	.59
Mar. 4	4	49	140	1.12	.33	.024	.028	.106	.60	.61
Mar. 4– 5	19	10	75	1.27	.74	.014	.014	.080	.50	.57
Mar. 5	3	24	....	....	....	....	....	....	....	....
Mar. 5	7	2	92	1.46	.93	.046	.017	.053	.54	.69
Mar. 5 6	22	46	67	1.61	.94	.026	.012	.037	.58	.79
Mar. 6– 7	14	56	61	1.63	1.06	.032	.013	.031	.56	.79
Mar. 7	10	11	62	1.62	1.01	.060	.009	.029	.57	.65
Mar. 7– 8	14	41	62	1.61	1.08	.046	.009	.029	.56	.60
Mar. 8– 9	23	12	65	1.61	1.10	.041	.008	.026	.54	.57
Mar. 9	9	57	64	1.70	1.12	.060	.009	.029	.62	.63
Mar. 9–10	14	1	76	1.68	1.19	.049	.011	.029	.61	.60
Mar. 10	8	42	69	1.60	1.11	.060	.012	.026	.58	.56
Mar. 10–11	15	53	68	1.56	1.05	.053	.011	.027	.57	.56
Mar. 11	8	19	59	1.52	1.06	.059	.011	....	.59	.58
Mar. 11–12	18	26	58	1.43	1.08	.029	.009	.024	.58	.58
Mar. 12–13	20	39	52	1.44	1.01	.053	.009	.024	.56	.60
Mar. 13–14	24	46	52	1.39	.92	.069	.013	.035	.56	.60
Mar. 14	7	5	62	1.48	.88	.096	.018	....	.64	.65
Mar. 14–15	18	10	61	1.47	.90	.085	.016	.092	.54	.58

TABLE 29.—*Amounts per hour of nitrogen constituents determined in urines of fasting steers*—Continued

Date and steer	Duration of period		Volume of urine	Total nitrogen	Urea-nitrogen	Ammonia-nitrogen	Amino-acid nitrogen	Hippuric-acid nitrogen	Preformed creatinine	Total creatinine
1924										
Steer D:	*hrs.*	*min.*	*c. c.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Feb. 27–Mar. 2	4 days		156	0.93	....	....	....	....	....	....
Mar. 2– 3	23	45	159	1.18	....	....	0.224	0.318	....	....
Mar. 3	1	45	193	1.24	0.41	0.091	.043	....	0.90	0.93
Mar. 3– 4	15	21	180	1.09	.37	.034	.032	.174	.70	.70
Mar. 4	8	50	423	1.34	.92	.047	.019	.138	.66	.70
Mar. 4– 5	15	2	67	1.29	.71	.020	.012	.072	.70	.64
Mar. 5	10	18	74	1.52	.91	.037	.014	.066	.70	.67
Mar. 5– 6	13	31	46	1.36	.77	.041	.010	.039	.65	.62
Mar. 6	10	38	175	1.72	.98	.132	.013	.045	.56	.61
Mar. 6– 7	13	22	93	1.30	.81	.056	.008	.028	.54	.52
Mar. 7	7	42	203	2.78	1.63	.123	.017	.054	1.03	1.01
Mar. 7– 8	16	20	95	1.82	1.23	.107	.010	.032	.67	.59
Mar. 8	7	43	82	1.86	1.11	.131	.015	.034	.65	.56
Mar. 8– 9	16	28	62	1.70	1.04	.078	.011	.027	.62	.63
Mar. 9	7	15	153	1.95	1.17	.104	.013	.030	.74	.76
Mar. 9–10	17	5	126	1.83	1.20	.105	.012	.026	.66	.66
Mar. 10	6	42	110	1.66	1.10	.095	.015	.025	.59	.60
Mar. 10–11	16	45	88	1.55	1.15	.066	.009	.023	.56	.57
Mar. 11	4	48	92	1.76	1.25	.107	.023	....	.62	.60
Mar. 11–12	20	30	84	1.59	1.14	.079	.012	.024	.68	.66
Mar. 12	6	57	257	2.25	1.41	.169	.018	.046	.94	.99
Mar. 12–13	15	7	66	1.14	.62	.060	.009	.032	.53	.57
Mar. 13	9	21	102	1.85	.93	.148	.019	.086	.88	.91
Mar. 13–14	16	31	59	1.02	.48	.091	.018	.083	.58	.61
Mar. 14	5	59	120	1.38	.48	.100	.020	.135	.72	.76
Mar. 14–15	16	13	259	1.07	.41	.056	.035	.171	.67	.69

	hrs.	min.	c. c.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
Steer E:										
Jan. 28–Feb. 11	12 days		87	0.88	....	....	....	....	....	....
Feb. 11–12	12 hrs.		58	.62	0.11	0.236	0.093	0.035	0.07	0.13
Feb. 12	12	..	94	1.03	....	....	.168	.063	.17	.33
Feb. 12	9	46	63	.67	.10	.153	.041	.093	.17	.24
Feb. 12–13	11	33	61	.63	.18	.101	.050	.095	.20	.26
Feb. 13–14	14	33	127	.83	.44	.063	.031	.059	.25	.30
Feb. 14	7	57	212	1.06	.70	.076	.015	.047	.27	.39
Feb. 14	2	15	642	1.80	1.22	.114	.025	.067	.42	.70
Feb. 14–15	14	4	46	.84	.52	.027	.006	.025	.26	.42
Feb. 15	9	31	50	1.09	.67	.042	.008	....	.28	.45
Feb. 15	10	25	159	1.34	.81	.069	.011	....	.35	.54
Feb. 15–16	2	46	201	1.54	.97	.131	.022	....	.30	.55
Feb. 16	7	19	232	1.33	....	....	.013	.025	.23	.45
Feb. 16	6	14	215	1.37	....	....	.035	.012	.25	.48
Feb. 16–17	11	37	137	1.32	.67	.145	.013	.026	.27	.47
Feb. 17	10	2	85	1.12	.60	.145	.019	.020	.24	.40
Feb. 17	6	30	76	1.69	.84	.129	.014	....	.54	.82
Feb. 17–18	16	2	38	.75	.41	.127	.048	.033	.17	.28
Feb. 18–19	14	4	69	.80	.17	.136	.064	.137	.20	.26
Feb. 19	12	51	79	.69	.18	.055	.064	.124	.24	.31
Feb. 19–20	11	26	87	.69	.13	.077	.058	.176	.28	.30
Feb. 20	13	24	96	.63	.07	.056	.051	.146	.27	.30
Steer F:										
Jan. 28–Feb. 11	13 days		71	.83	....	....	....	....	....	....
Feb. 11–12	12 hrs.		61	.75	.29	.104	.119	.163	.20	.25
Feb. 12	13	..	65	.89	.36	.095	.072	....	.23	.30
Feb. 12–13	9	16	76	.77	.15	.082	.047	.140	.25	.31
Feb. 13	11	10	....	....	....	....	....	....	....	....
Feb. 13	1	33	83	.95	.41	.123	.066	....	.34	.41
Feb. 13	2	32	58	.78	.16	.030	.019	....	.38	.44
Feb. 13–14	22	15	47	.82	.51	.029	.021	.048	.29	.34
Feb. 14	2	..	70	1.20	....	....	....	....	.40	.48
Feb. 14–15	20	..	38	.99	.57	.024	.008	.026	.30	.48
Feb. 15	4	50	46	1.28	.46	.027	.005	....	.34	.58
Feb. 15–16	18	21	46	1.40	.91	.054	.011	.022	.37	.58
Feb. 16	6	24	45	1.36	.86	.066	.005	....	.32	.50
Feb. 16–17	18	43	48	1.43	1.00	.074	.007	.019	.38	.56
Feb. 17	6	31	45	1.27	.88	.081	.006	....	.30	.43
Feb. 17–18	18	1	61	1.32	.94	.090	.009	.018	.31	.44
Feb. 18	5	0	56	1.61	.45	.111	.013	....	.44	.67
Feb. 18–19	20	5	46	1.15	.58	.076	.011	.037	.29	.45
Feb. 19–20	11	4	74	1.05	.56	.090	.023	.114	.30	.33
Feb. 20	12	36	54	.66	.23	.059	.020	.106	.20	.22

mately 24 hours long. Hence the total daily amounts are reasonably comparable from day to day. The large differences in the time intervals occasionally found must, however, always be held in mind in making any final deductions. In the fasts in November 1923, recorded in Table 29, the 24-hour period of collection was likewise adhered to reasonably closely. In the 1924 fasts the collections were made more frequently, and in Table 29, therefore, the length of each period is given in hours and minutes.

Since it was impossible in these fasts to secure sharply divided 24-hour or 12-hour periods, it has seemed best to discuss the chemistry of the urine in all of the different fasts on the basis of the amounts per hour. Aside from the total excretion of nitrogen, which is of chief interest in connection with the protein loss, the chemical analysis of the urine is of the greatest value in indicating the proportions of the various ingredients excreted and the changes in these relationships as the fasts progressed. Hence in practically all cases the expression of the results on the per hour basis is reasonably satisfactory. Logically there is no reason for adhering to the 24-hour period, since fasting brings about a change in the metabolic level which takes place from hour to hour as well as from 24 hours to 24 hours. Hence the hourly values reported in Table 29 for the later fasts present a much more intelligent picture of the course of the excretion of the different urinary constituents.

In addition to the study of the urine during the fasting periods proper, analyses were also made during the feed periods preceding and following the fasts. The data for these feed periods are likewise recorded in Tables 28 and 29, being separated from the fasting data by horizontal lines. In Table 28 the total volume of urine during these feed periods is given in kilograms instead of in liters, and the volume of urine per hour is given in grams instead of in cubic centimeters, as indicated at the head of the columns in the table.

One must realize, in analyzing these data, that the fasts in November followed pasture feeding and that prior to all the other fasts, with the exception of those in February and March 1924, the steers had been receiving an approximately maintenance ration of hay and meal. In the 1924 fasts all four steers had been for a considerable period of time on a low nutritive plane.

Discussion of Results

CHLORIDES IN URINE

In the first few fasts of steers C and D, information was secured regarding the chlorides in urine, as shown in Table 28. Since the chloride excretion is dependent in large part upon the intake, the rapid fall noted in this excretion during the fasting periods is not surprising. The excretion drops off enormously, until the hourly values become as low, in one instance, as 13 mg. Owing to the necessity for using hydrochloric acid to preserve the urines, it was, unfortunately, impossible to study the chloride excretion during the fasts at the submaintenance level.

NITROGEN EXCRETED IN URINE PER HOUR

Nitrogen is the most characteristic chemical element in urine and for decades has been considered to be an essential index of protein metabolism. The nitrogen excretion per hour is recorded in both Table 28 and Table 29. The probable 24-hour excretion will be considered subsequently (see pp. 127 to 129) in connection with the discussion of the daily loss of nitrogen both in the urine and in the feces, but the hourly rate of excretion is of immediate importance.

Prior to the fasts the hourly excretion of nitrogen by steers C and D is not far from 2.5 to 4.5 grams, except prior to the fasts in March 1924, at the submaintenance level, when the hourly output is much lower. Similarly, with steers E and F the influence not only of submaintenance feeding but of smaller body-weights results in a low hourly output, even prior to the fast. The important influence of the preceding ration upon the hourly nitrogen excretion is shown in the fasts in March 1924 with steers C and D, when the body-weights at the beginning of the fasts were about 600 kg. As a matter of fact, the body-weights were the third highest in the long series of fasts with these two animals, and yet the nitrogen per hour is lower in this fast than in any of the preceding fasts. Following submaintenance feeding, there is a gradual increase in the nitrogen excretion in the first four days of fasting, but in the fasts following maintenance feeding the nitrogen has a tendency to fall off as the fast progresses. The minimum values with both animals are found, as is to be expected, in the fasts at the submaintenance level, when the excretions of both steers settle down to approximately 1.6 and 1.8 grams per hour. This corresponds to not far from 40 grams per 24 hours. If the urinary nitrogen excretion of a man weighing approximately 60 kg., or one-tenth of what these steers weighed, is assumed to be one-tenth of the minimum nitrogen excretion noted with these steers, it would be about 4.0 grams. This is about as low a value as has ever been found with man, except for the values obtained by Petrén[a] with his diabetic patients on a diet high in fat and low in protein. The taking of food following these fasting experiments almost invariably lowered the nitrogen output even below that of the last day of the fast, due in all probability to the storage of nitrogen to replenish the loss and to the protective action of the carbohydrate.

That the excretion of nitrogen was essentially independent of the volume of urine is brought out by the comparison of the volume of urine excreted per hour and the actual nitrogen output. A typical instance is the comparison for steer C in the fast in January 1922. On the fifth day, January 8–9, the volume was 78 c. c. per hour and on the next day it was more than double, i. e., 165 c. c., but the nitrogen output, on the contrary, decreased from 2.31 to 2.27 gm. per hour. In most of the fasts the nitrogen excretion either remains at a fairly constant level or gradually decreases, irrespective of the volume of urine, and thus there is not a "washing-out" effect of previously metabolized nitrogenous products. Even on the low metabolic plane in the March fasts great variations in the volume of urine are found with a

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[a] Petrén, Proc. XI Internat. Physiol. Congress, Edinburgh, 1923; ibid., Diabetes-Studier, Copenhagen, 1923, p. 545.

fairly constant level of nitrogen excretion, a greater irregularity being noted with steer D than with steer C. With steers E and F, an indication of a relationship between the volume of urine and the nitrogen excretion is frequently found. For example, on February 14 the volume of urine excreted by steer E per hour is 642 c. c. and the nitrogen per hour is 1.80 gm. The period is, to be sure, short. During the next period of 14 hours and 4 minutes the volume per hour is only 46 c. c. and the nitrogen output is 0.84 gm., or one-half that of the preceding period. There is, in this instance, a decrease in both factors, but in no sense a strict relationship between the two.

From this experience and from that of Forbes, Fries, and Kriss,[a] one might suggest that when it is desirable to study the periodic variations in the nitrogen output after the ingestion of food or the hourly variations in the urine even during fasting, preliminary experiments with animals should be made and an animal selected which shows regularity in nitrogen excretion. It is evident in our series of fasts, for example, that steer C is extraordinarily regular in the voiding of the nitrogen constituents, irrespective of the quantity of the urine. One might infer that at each voiding the bladder was reasonably well emptied and that physiologically the animal functioned regularly. Steer F was likewise regular, but steers D and E show considerable variability in the excretion of the urinary constituents. Further consideration of the nitrogen output may best be made when the apportionment of the nitrogen among its various constituents is studied.

PARTITION OF URINARY NITROGEN

In the fasts of steers C and D in November 1923, the combined urea-nitrogen and ammonia-nitrogen decreases as the fast progresses. (See Table 29.) A striking fall in the amino-acid nitrogen and the hippuric-acid nitrogen was observed, particularly after the first day. The results for the preformed and total creatinine are hardly interpretable without reference to the total nitrogen excretion on the same day, but they both remain high, with little indication of a falling off. In the fasts in March 1924, at the submaintenance level, the urea-nitrogen and the ammonia-nitrogen are separated for the first time, and it is clear from these results that there is a distinct tendency for the urea-nitrogen to increase and for the ammonia-nitrogen to remain essentially constant after the first two or three days.

The amino-acid nitrogen in the case of steer C drops off markedly during fasting, as does the hippuric-acid nitrogen, but the preformed and total creatinine remain fairly constant. After the fast, when food is given, little change takes place except that the urea-nitrogen decreases somewhat and the ammonia-nitrogen increases. With steer D the picture is not unlike that with steer C, namely, a rise in the urea-nitrogen, a tendency for a slight increase in the ammonia-nitrogen, a rapid decrease in the amino-acid and the hippuric-acid nitrogen, and essential constancy in the creatinine. With refeeding there is a striking fall in the urea-nitrogen of steer D. The ammonia-nitrogen tends to remain about constant and the amounts of amino-acid and hippuric-acid nitrogen tend to increase. There is no striking change in the creatinine.

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[a] Forbes, Fries, and Kriss, Journ. Dairy Sci., 1926, 9, p. 15.

TABLE 30.—*Partition of nitrogen excreted in urines of fasting steers*

Date and steer	Proportion of total nitrogen in—					
	Urea	Ammonia	Amino acids	Hippuric acid	Preformed creatinine	Total creatinine
Steer C: 1923	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Nov. 5– 6	75.9		1.0	3.7	5.4	8.1
Nov. 6– 7	77.9		.5	2.2	5.2	9.2
Nov. 7– 8	82.7		.4	1.4	6.5	11.2
Nov. 8– 9	81.0		.4	1.3	8.3	10.5
Nov. 9–10	74.1		.6	1.5	9.3	10.8
Steer D:						
Nov. 5– 6	78.9		2.0	3.4	5.9	8.4
Nov. 6– 7	82.2		.3	2.0	7.1	10.3
Nov. 7– 8	65.7		.4	1.6	7.4	10.9
Nov. 8– 9	74.1		.3	1.3	8.7	10.3
Nov. 9–10	74.7		.3	1.8	7.9	9.7
Steer C: 1924						
Mar. 2– 3	38.3		17.8	27.5	18.0	20.0
Mar. 3	26.4	6.7	6.0	....	22.9	23.8
Mar. 3– 4	40.1	2.1	3.0	8.9	25.3	27.7
Mar. 4	29.1	2.2	2.5	9.5	20.0	20.2
Mar. 4–5	58.4	1.1	1.1	6.3	14.7	16.8
Mar. 5	[1]51.6	[1]4.6	[1]1.5	....	[1]12.9	[1]17.6
Mar. 5	63.6	3.2	1.2	3.6	13.8	17.6
Mar. 5–6	58.7	1.6	.7	2.3	13.4	18.3
Mar. 6–7	64.7	2.0	.8	1.9	12.6	18.0
Mar. 7	62.4	3.7	.5	1.8	13.0	14.8
Mar. 7–8	67.0	2.8	.6	1.8	12.9	13.7
Mar. 8–9	68.6	2.6	.5	1.6	12.6	13.1
Mar. 9	66.2	3.5	.5	1.7	13.5	13.8
Mar. 9–10	71.1	2.9	.7	1.7	13.6	13.3
Mar. 10	69.3	3.7	.7	1.6	13.5	13.1
Mar. 10–11	66.9	3.4	.7	1.7	13.5	13.3
Mar. 11	70.0	3.9	.7	....	14.5	14.3
Mar. 11–12	75.5	2.0	.7	1.7	15.0	15.1
Mar. 12–13	70.1	3.7	.6	1.7	14.6	15.5
Mar. 13–14	66.0	5.0	.9	2.5	15.1	16.1
Mar. 14	59.2	6.5	1.2	....	16.0	16.2
Mar. 14–15	61.1	5.8	1.1	6.2	13.6	14.7
Steer D: 1924						
Mar. 2–3	34.7		18.9	26.8	....	....
Mar. 3	33.2	7.3	3.5	....	26.9	27.7
Mar. 3–4	34.3	3.1	2.9	16.1	23.8	24.0
Mar. 4	68.4	3.5	1.4	10.3	18.3	19.5
Mar. 4–5	54.7	1.5	1.0	5.6	20.1	18.5
Mar. 5	59.9	2.5	.9	4.3	17.2	16.3
Mar. 5–6	57.0	3.0	.7	2.9	17.8	17.0
Mar. 6	57.0	7.7	.7	2.6	12.2	13.2
Mar. 6–7	61.9	4.3	.6	2.2	15.3	14.7
Mar. 7	58.8	4.4	.6	1.9	13.8	13.6
Mar. 7–8	67.6	5.9	.5	1.8	13.7	12.1
Mar. 8	59.5	7.0	.8	1.8	13.0	11.3
Mar. 8–9	61.2	4.6	.6	1.6	13.5	13.7
Mar. 9	59.8	5.3	.6	1.5	14.0	14.5
Mar. 9–10	65.6	5.7	.7	1.4	13.4	13.4
Mar. 10	66.4	5.7	.9	1.5	13.1	13.5

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[1] The urine collected for steer C during this period was all that could be caught. It is estimated to be about one-third of the total urination.

TABLE 30.—*Partition of nitrogen excreted in urines of fasting steers*—Continued

Date and steer	Proportion of total nitrogen in—					
	Urea	Ammonia	Amino acids	Hippuric acid	Preformed creatinine	Total creatinine
Steer D—*Cont.* 1924.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
Mar. 10–11	74.4	4.2	0.6	1.5	13.4	13.6
Mar. 11	71.2	6.1	1.3	....	13.1	12.7
Mar. 11–12	71.5	5.0	.8	1.5	15.9	15.4
Mar. 12	62.8	7.5	.8	2.1	15.5	16.2
Mar. 12–13	53.9	5.2	.8	2.8	17.3	18.4
Mar. 13	50.1	8.0	1.0	4.7	17.6	18.3
Mar. 13–14	47.1	8.9	1.8	8.2	21.1	22.0
Mar. 14	34.7	7.2	1.4	9.8	19.3	20.5
Mar. 14–15	38.7	5.2	3.2	15.9	23.2	23.9
Steer E:						
Feb. 11–12	18.2	38.1	15.0	5.6	4.2	8.0
Feb. 12	....	....	16.3	6.1	6.2	11.9
Feb. 12	15.6	22.7	6.2	13.8	9.2	13.5
Feb. 12–13	28.2	16.2	7.9	15.2	11.8	15.5
Feb. 13–14	53.3	7.6	3.8	7.1	11.3	13.5
Feb. 14	66.0	7.2	1.4	4.4	9.3	13.8
Feb. 14	68.1	6.3	1.4	3.7	8.6	14.5
Feb. 14–15	62.1	3.2	.7	3.0	11.3	18.3
Feb. 15	61.1	3.9	.7	....	9.6	15.1
Feb. 15	60.5	5.2	.9	....	9.6	15.1
Feb. 15–16	62.9	8.5	1.4	....	7.3	13.2
Feb. 16	....	....	1.0	1.8	6.4	12.6
Feb. 16	....	....	2.6	.9	6.7	13.0
Feb. 16–17	50.4	10.9	1.0	1.9	7.6	13.2
Feb. 17	53.9	12.9	1.7	1.8	8.1	13.4
Feb. 17	50.0	7.6	.8	....	11.9	18.0
Feb. 17–18	[1] 54.8	[1] 17.0	[1] 6.3	[1] 4.5	[1] 8.4	[1] 13.6
Feb. 18–19	21.6	16.9	8.0	17.1	9.2	12.1
Feb. 19	25.7	8.1	9.3	18.0	12.7	16.6
Feb. 19–20	19.6	11.2	8.4	25.6	14.9	16.3
Feb. 20	11.2	9.0	8.1	23.2	16.2	17.8
Steer F:						
Feb. 11–12	38.5	13.9	15.9	21.7	9.7	12.4
Feb. 12	39.9	10.7	8.1	....	9.5	12.3
Feb. 12–13	19.2	10.6	6.1	18.2	12.2	15.1
Feb. 13	[2] 25.5	[2] 11.4	[2] 4.8	....	[2] 14.2	[2] 17.6
Feb. 13	42.8	12.9	7.0	....	13.1	16.2
Feb. 13	20.2	3.8	2.5	....	18.2	20.8
Feb. 13–14	62.6	3.5	2.6	5.9	13.0	15.4
Feb. 14	....	....	....	....	12.4	14.9
Feb. 14–15	57.0	2.4	.8	2.6	11.2	17.9
Feb. 15	36.2	2.1	.4	....	9.7	16.8
Feb. 15–16	64.9	3.9	.8	1.6	9.7	15.4
Feb. 16	63.4	4.9	.4	....	8.7	13.8
Feb. 16–17	70.1	5.2	.5	1.3	10.0	14.6
Feb. 17	69.2	6.4	.4	....	8.7	12.5
Feb. 17–18	71.5	6.8	.7	1.3	8.7	12.4
Feb. 18	28.2	6.9	.8	....	10.2	15.4
Feb. 18–19	50.3	6.6	.9	3.2	9.3	14.7
Feb. 19–20	52.7	8.5	2.1	10.8	10.6	11.7
Feb. 20	35.8	8.9	3.0	16.1	11.1	12.7

[1] This urine was contaminated by a small amount of feces.

[2] This urine is only a portion of the urine for the period. About 300 grams of urine were lost.

The younger animals in their fast at the submaintenance level presented a different picture in some ways. The findings are essentially the same for both steers. In the first place, the total amount of nitrogen varies considerably. There is a tendency for the urea-nitrogen to increase. There is great variability in the ammonia-nitrogen, a decrease in the amino-acid and hippuric-acid nitrogen, and a striking increase in the creatinine, both preformed and total. The considerable difference between the preformed and total creatinine indicates that these animals excreted creatine. When feed is given after the fast, there is a great fall in the total nitrogen per hour, a decrease in the urea-nitrogen and the ammonia-nitrogen, an increase in the amino-acid and hippuric-acid nitrogen, essential constancy in the preformed creatinine, and a great decrease in the total creatinine, particularly after the first period of refeeding.

Since the total nitrogen excretion changed during fasting, a more careful interpretation of these changes in the nitrogenous ingredients can be secured only by a study of the proportion of nitrogen excreted in the various forms and the changes in these proportions as time goes on. The data for this study are shown in Table 30.

Urea and ammonia-nitrogen—From an examination of the distribution of the nitrogen it is seen that during fasting the urea-nitrogen becomes a greater proportion of the total urinary nitrogen than it is during feeding, and that with the resumption of food the urea becomes a smaller proportion of the total nitrogen eliminated. Unfortunately, the only experiments in which the urea-nitrogen was determined by itself are in the fasts with the four animals in 1924, at the submaintenance level. In the November fasts in 1923 the proportion of total nitrogen in the combined urea and ammonia-nitrogen remains essentially constant as the fast progresses. In the 1924 fasts, on the contrary, the nitrogen from urea rises rapidly from 26 per cent on March 3 with steer C to 70 per cent or over at the end of the fast. Low proportions are noted in the fasts with the other animals likewise, from as low as 33 per cent with steer D to 15 per cent with steer E and 19 per cent with steer F. In the case of all four animals the percentage of urea-nitrogen rises as the fast progresses, approaching finally a proportion that is commonly found with humans or carnivorous animals subsisting upon a nitrogen-free diet. The subsequent taking of food in these experiments has a most profound effect upon this proportion in that after the first two days the percentage of urea-nitrogen tends to be low, corresponding to the initial values. The ammonia-nitrogen was likewise determined in the four experiments at the submaintenance level. The values during the fasts are low in general, and suggest that there was no particular call for extra ammonia to neutralize any acid formation. For the most part the figures are regular in all four fasts. It is a noticeable fact that with all the steers the taking of food in practically every case raises the proportion of ammonia-nitrogen excreted in urine. In certain instances, notably in the experiment with steer E prior to the fast and even on the first day of the fast, the very high ammonia values suggest the possibility that the urine may have decomposed.

Hippuric-acid nitrogen—In this determination one obtains the amount of benzoic acid present, and one must assume that the nitrogen was combined with benzoic acid to form hippuric acid. We have already seen that there is a tendency for the amount of hippuric-acid nitrogen to decrease as the fast goes on. This is also shown by the percentage values, which fall appreciably. With the resumption of feeding the values increase again. The absolute values for hippuric-acid nitrogen excreted by all four of these animals, as shown in Table 29, are closely alike during the fasting-periods. It seems singular that animals with such large differences in body-weight should have such uniformity in this excretion. Indeed, this finding suggests that there is a constancy in the hippuric acid eliminated, indicating that it is of endogenous origin.

Preformed creatinine—Folin[a] attracted the attention of physiologists to the significance of creatinine in protein metabolism. The existence of creatinine in the body in the form of creatine and creatinine and the fact that creatine has been found in the urines of fasting humans led to our determining both in these samples. As has been already pointed out, the total amount of preformed creatinine remains relatively constant with the adult animals. This holds true to a certain extent with the total creatinine also, but the younger animals show very different reactions and indicate a considerable excretion of creatine as such. The creatinine elimination of steers E and F is smaller than that of the larger steers, C and D. The percentage of the total nitrogen in the form of preformed creatinine was fairly constant in the fast in November 1923, with a tendency to increase. On the contrary, in the fasts at the submaintenance level, particularly with the two older animals, there was a distinct decrease in the percentage of nitrogen excreted in this form as the fast progressed.

Total creatinine—The total creatinine expresses the preformed creatinine plus any creatine which has been converted by hydrolysis into creatinine. In the November fasts of 1923 there is a distinctly greater amount of total creatinine than preformed creatinine, showing excretion of creatine as such. In the fasts of the larger animals in 1924, at the submaintenance level, a difference between the preformed and the total creatinine is to be found only during the first part of the fast. With steers E and F the differences between preformed and total creatinine are more marked than with steers C and D in the fasts after submaintenance feeding. Indeed, a considerable proportion of the creatinine is in the form of creatine. The difference between the two creatinines actually persists for some little time, even after food is taken. It thus seems that the smaller animals were much more affected by fasting, as evidenced by the increasing elimination of creatine, but with the larger animals the data would suggest that during feeding there was a constant elimination of creatine.

Creatine—From the findings with steers C and D in the fasts in November 1923, that is, after full pasturage, when a rather striking excretion of creatine is shown, one could argue that *on feed* there is a regular excretion of creatine, which disappears when the animal fasts at a lower nutritive plane. This is contrary to the experience with humans, with whom as the fast progresses there is an increased excretion of creatine. The appearance of creatine in the urine *during feeding*, particularly in the case of the two

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[a] Folin, Am. Journ. Physiol., 1905, 13, p. 83.

smaller steers, prior to the fast and shortly after refeeding, was again rather unusual. Dr. Carpenter suggests that this may be due not to the fact that creatine is a metabolic product but to the fact that the urine actually decomposes in the bladder of the animal before it is voided. When one recalls that the urines of herbivora are highly alkaline, it does not seem impossible that the retention of such a fluid at body-temperature might result in the change from creatinine to creatine. As a matter of fact, one of Carpenter's experiments has shown that when creatinine was added to one of these urines it disappeared quickly. After the urine is voided, therefore, it is practically impossible to keep the creatinine for any considerable length of time. This suggestion is of interest and of importance because it points to the possibility of the composition of freshly voided urine being due not solely to the constituents secreted but to a chemical change towards an equilibrium which takes place before the urine is voided. Thus, it is more than likely that when one is dealing with the composition of urine from such animals, one must consider that the reaction of the urine *before* it is voided and the length of time it remains in the bladder will affect the actual chemical nature of the excreted liquid. A striking point in connection with the creatine is that throughout the fasts with steers E and F there was a continual excretion, which was contrary to the finding with steers C and D. One explanation may be that the reserve stores of these two animals, E and F, were not sufficient to supply an adequate portion of the energy due to carbohydrate and fat, so that these two younger animals gradually had to call upon their store of protein and this disintegration of tissue resulted in the liberation of creatine.

OTHER URINARY CONSTITUENTS

For a detailed discussion of the various forms of sulphur, phenols, acid bodies, fixed bases, and organic acids reference must be made to Dr. Carpenter's more complete treatment of these data. Extraordinarily small amounts of phosphorus were found, so that excretion of phosphorus in the urine can hardly be considered of any significance in the fasting steer. The phenols, which serve as indications of a putrefactive change along with the ethereal sulphates, decrease rather rapidly as the fast progresses, although it is to be borne in mind that there are a number of putrefactive changes in the intestinal tract for a considerable time after the last feed has been given. The acid bodies, acetone and diacetic acid, and β-oxybutyric acid, were present under practically all conditions, but frequently only in traces. The important thing is that these acid bodies were likewise noted on food days, and hence the conclusion is reached that fasting, contrary to the conditions with humans, does not alter the excretion of these bodies with steers.

TOTAL NITROGEN EXCRETION PER KILOGRAM OF BODY-WEIGHT PER 24 HOURS

In the consideration of these fasts thus far particular stress has been laid upon the influence of the fast upon the nitrogen excretion from hour to hour as the fast progresses. These animals had varying body-weights, steers C and D being larger than the younger steers, E and F. The nitrogen excreted per kilogram of body-weight is therefore of interest. With the two large animals, C and D, the nitrogen-level is much the same. In the case of steer C, for example, the values vary from as high as 0.237 to as low as 0.074 gm. at the end of the tenth day in the fast in January 1922, and in the April fast of 1922 a value as low as 0.073 gm. was found on the tenth day. The values noted in the fasts at the submaintenance level are much lower than those in the fasts at the maintenance level. Indeed, with steer C a very low value of 0.032 gm. is noted in the March fast, the highest value being 0.067 gm. Similarly, with steer D, very low values are observed during the March fast following submaintenance feeding, the lowest value being 0.042 gm. With the younger animals, E and F, the nitrogen per kilogram of body-weight per 24 hours during the fasting period is perceptibly high and has a distinct tendency to *increase* as the fast progresses. Contrary to the observations on the larger steers, this suggests that the reserves in the smaller animals were not so great, and consequently the demand for energy supply was met by an increasing utilization of body protein. This belief is confirmed by the fact that the taking of food greatly decreases the excretion of nitrogen per kilogram of body-weight per 24 hours. Thus, in the case of steers C and D there was a slight decrease after the ingestion of food, and with steers E and F there was a noticeable decrease.

CREATININE COEFFICIENT

The relationship between the total amount of preformed creatinine and the body-weight of the animal has attained considerable importance, that is, the actual number of milligrams of preformed creatinine per kilogram of body-weight per 24 hours. This relationship has been computed for the four fasts in 1924 at the submaintenance level, and has been found to remain relatively constant throughout the fast. In the case of steer C, 27.2 mg. of preformed creatinine were excreted per kilogram of body-weight per 24 hours on the day before the fast, March 2–3. On the first day of the fast this ratio fell to 21 mg. and was relatively constant throughout the fast. During the two days following the fast there was likewise no appreciable alteration. Indeed, with both animals the creatinine coefficient was reasonably constant when computed on the basis either of preformed creatinine or total creatinine. With the younger steers, E and F, however, although the preformed creatinine per kilogram of body-weight remains essentially constant, the coefficient for the total creatinine becomes appreciably higher as creatine is excreted. The two younger animals agree between themselves, but show distinctly higher coefficients than do the two adult animals.

THE NITROGEN ECONOMY OF STEERS

Unfortunately, the method for determining hippuric acid is really a method for determining benzoic acid. Consequently, we do not know whether there may not have been a hydrolysis of the hippuric acid in the bladder, so that free amino-acid was formed and subsequently determined in the amino-acid determination. If this amino-acid was not free, but was combined with the benzoic acid, then besides free amino-acid considerable amounts of nitrogen were eliminated in the form of combined amino-acid with the benzoic acid. Because of the low digestibility of many of the feedstuffs, particularly the roughage and grasses used by herbivora, and because of the relatively large amounts of nitrogen liberated in the form of amino-acid, whether free or combined with benzoic acid, the efficiency of the utilization of nitrogen by the steer is extremely low. Consequently, as a source of obtaining protein economically from the nitrogen cycle, these animals are seemingly very inefficient. When the formation of protein or the addition of muscle, or protein storage, is the main object of feeding, it seems from the results of these urine analyses that it is of the highest importance to know what proportion of the nitrogen escaped into the urine in a form which was not available for metabolic processes, namely, in the amino-acid form and as hippuric or benzoic acid combined with amino-acid. It therefore should be important to determine which type of ration results in the more economical use of the protein ingested, a ration composed only of roughages, such as hays and grasses, or a ration composed of a roughage combined with a grain or meal mixture.

Studies are needed in which the hippuric acid *as such* is determined, as well as the benzoic acid, in order to determine whether it is eliminated in the combined or free form, together with the determination of amino-acid as such by the regular amino-acid method. These animals were on an extremely low nitrogen-level. Possibly with a higher nitrogen-level a larger proportion of nitrogen might be eliminated as urea and relatively less as amino-acid and hippuric acid. It can be seen from the course of the percentage distribution, however, that as the animal tends to live more and more on its own body-substance, the composition of the urine and the distribution of the urinary nitrogen become more like that in the human being. It would seem that the nearer the ruminant was to its natural condition of food intake, proportionately greater was the loss in nitrogen in forms which had not undergone metabolic changes or had not become an integral part of the body.

GENERAL CONCLUSIONS WITH REGARD TO THE COMPOSITION OF STEER'S URINE DURING FASTING

Prior to fasting, herbivorous animals are subsisting upon a ration strikingly different from the body substances. During fasting the large ballast in the alimentary tract supplies certain materials for some time, but as the ballast becomes exhausted, the animal gradually begins to subsist solely upon its own tissue deposits and hence, in a certain sense, becomes a carnivorous animal. During the considerable period of time, possibly 7 days, when the ballast is passing through the alimentary tract, the animal is gradually changing from a condition in which it existed entirely on vegetable food to one of fasting, i. e., subsisting solely on its own body-tissue. At the beginning the urine is alkaline. Gradually, however, its high alkalinity disappears, and in general after 4 or 5 days the urine reacts acid to litmus paper. During this period the most marked change in the character of the urine is in the distribution of the nitrogen. At first, owing to the preponderance of food residue in the intestines, the materials in the urine are derived in part directly from the food. With ruminants one of the most characteristic of these materials is hippuric acid, but as the effect of the previous food disappears, the hippuric acid greatly diminishes. On the contrary, urea, which is found in the urine of humans and carnivora in a much higher percentage, is very low in steer's urine when he subsists on food, and one of the first striking changes in steer's urine during fasting is a reversal of the proportions between these two constituents, that is, a lowering of the nitrogen due to hippuric acid and a gradual increase in the nitrogen due to urea. In the fasts at the submaintenance level the percentage values for urea finally approach those found for the urines of man. These figures, together with the estimate of a comparable nitrogen figure per 24 hours for man, indicate that the animals were on a very low nitrogen plane, due to the submaintenance feeding. A further indication of the low nitrogen-level is suggested by the relatively high percentage of nitrogen due to creatinine. The quantitative elimination of preformed creatinine, as Folin has shown,[a] is independent of the nitrogen-level; therefore, the lower the nitrogen-level the higher is the percentage of preformed creatinine nitrogen. Thus, in the fasts of steers C and D after pasture in November 1923, the preformed creatinine nitrogen was from 5 to 9 per cent of the total nitrogen excretion. In the March fasts at the submaintenance level it was from 12 to 27 per cent, but the amounts per hour were nearly the same in these two fasts with each steer. Likewise the amino-acid was relatively high at the start, and then fell to a low figure.

Another feature of the urines of these herbivora during fasting is the very low ammonia-content. Man develops acidosis during fasting, but herbivora do not, for they excrete extraordinarily small amounts of acetone bodies and β-oxybutyric acid. Even the younger animals, E and F, show a similar resistance to the effect of fasting, so far as the development of acidosis and ketonuria is concerned. The respiratory quotients of these animals, as will be seen later (see pp. 157 to 161), approached the quotient indicating a combustion of pure fat, hence seemingly an ideal condition for the development of ketonuria. Obviously, it is not a universal biological phenomenon that ketone bodies are developed when the proportion of carbohydrate to fat is low. This has great significance in the study of the keto and anti-ketogenic ratio, such as is being applied clinically with man. Dr. Carpenter suggests that it may be questioned whether the cause of and development of ketosis on the part of man is due to the low proportion of carbohydrate or is due to the character of the material which is drawn upon when the carbohydrate in the diet is diminished. It is difficult to understand why man should differ in this respect from other animals, which in their metabolism show other characteristics which are similar to those noted with man. The problem really demands attention from a standpoint other than that of the pure relationship of carbohydrate to fat.

In comparing these experiments on steers with those on obese humans it seems that the ability to use fat and not develop acidosis is present when there is a low nitrogen excretion. This is in full conformity with Petrén's experience with diabetics on diets high in fat and low in protein.[b] The question arises as to whether the utilization of fat, in protein and carbohydrate withdrawal, is not actually favored by a low nitrogen-level.

The proportion of total nitrogen excreted as creatinine may be used as an indication of the nitrogen-level, that is, the lower the proportion of nitrogen

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[a] Folin, Am. Journ. Physiol., 1905, **13**, p. 84.

[b] Petrén, Proc. XI Internat. Physiol. Congress. 1923; ibid., Diabetes-Studier. Copenhagen, 1923.

TABLE 31.—*Total nitrogen loss during fasts of 5 to 14 days*[1]

Date	Steer C			Steer D		
	Nitrogen in urine	Nitrogen in feces	Total nitrogen loss	Nitrogen in urine	Nitrogen in feces	Total nitrogen loss
1921	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Nov. 26 to Dec. 6	(59.4)	.....	.....	(57.5)	.....	.....
Dec. 6– 7	64.7	(62.6)	127.3	49.3	(71.8)	121.1
Dec. 7– 8	60.0	(26.3)	86.3	50.7	(18.2)	68.9
Dec. 8– 9	81.5	(21.2)	102.7	48.3	(7.3)	55.6
Dec. 9–10	42.3	(6.0)	48.3	61.2	(14.8)	76.0
Dec. 10–11	50.8	(6.4)	57.2	[2] 32.7	(6.0)	38.7
Dec. 11–12	55.5	(5.8)	61.3	53.1	(8.8)	61.9
Dec. 12–13	42.7	(4.6)	47.3	50.7	(6.9)	57.6
Total	397.5	(132.9)	530.3	346.0	(133.8)	479.8
1922						
Dec. 22 to Jan. 4	(95.5)	.....	.....	(101.5)	.....	.....
Jan. 4– 5	123.0	65.1	188.1	122.0	61.0	183.0
Jan. 5– 6	118.0	26.2	144.2	89.9	28.4	118.3
Jan. 6– 7	89.8	14.5	104.3	85.4	11.1	96.5
Jan. 7– 8	44.2	6.6	50.8	66.8	8.4	75.2
Jan. 8– 9	66.9	8.1	75.0	57.0	7.4	64.4
Jan. 9–10	62.3	6.2	68.5	49.9	5.2	55.1
Jan. 10–11	37.1	6.5	43.6	55.7	6.9	62.6
Jan. 11–12	43.6	3.5	47.1	37.8	4.9	42.7
Jan. 12–13	30.4	2.9	33.3	32.2	4.0	36.2
Jan. 13–14	44.7	3.1	47.8	35.6	3.0	38.6
Total	660.0	142.7	802.7	632.3	140.3	772.6
Mar. 31 to Apr. 17	(72.3)	.....	.....	(76.7)	.....	.....
Apr. 17–18	78.2	60.7	138.9	91.1	63.6	154.7
Apr. 18–19	75.2	23.8	99.0	88.9	22.4	111.3
Apr. 19–20	67.8	16.0	83.8	78.7	16.4	95.1
Apr. 20–21	78.6	12.3	90.9	71.1	12.7	83.8
Apr. 21–22	57.9	8.2	66.1	62.3	4.8	67.1
Apr. 22–23	63.9	8.3	72.2	56.5	9.3	65.8
Apr. 23–24	42.9	5.3	48.2	38.9	6.1	45.0
Apr. 24–25	48.8	8.1	56.9	44.0	5.1	49.1
Apr. 25–26	52.3	3.7	56.0	38.3	4.6	42.9
Apr. 26–27	34.3	2.6	36.9	45.1	3.9	49.0
Apr. 27–28	51.9	7.1	59.0	35.0	4.3	39.3
Apr. 28–29	36.3	4.0	40.3	37.3	3.7	41.0
Apr. 29–30	39.7	3.9	43.6	35.8	3.0	38.8
Apr. 30–May 1	47.2	3.5	50.7	33.9	2.2	36.1
Total	775.0	167.5	942.5	756.9	162.1	919.0
May 9 to June 1	(80.0)	.....	.....	(82.7)	.....	.....
June 1– 2	100.0	68.6	168.6	93.8	61.7	155.5
June 2– 3	103.0	32.9	135.9	96.2	27.5	123.7
June 3– 4	80.5	19.0	99.5	88.1	20.8	108.9
June 4– 5	62.0	7.2	69.2	66.1	7.1	73.2
June 5– 6	60.8	9.3	70.1	62.9	10.2	73.1
Total	406.3	137.0	543.3	407.1	127.3	534.4

[1] Values in parentheses are based upon analyses of composite samples; all others are based upon daily samples.

[2] Some urine lost; amount not known.

TABLE 31.—*Total nitrogen loss during fasts of 5 to 14 days*[1]—Continued

Date	Steer C			Steer D		
	Nitrogen in urine	Nitrogen in feces	Total nitrogen loss	Nitrogen in urine	Nitrogen in feces	Total nitrogen loss
1922	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Nov. 6– 7	[2] 99.0	47.2	146.2	99.4	47.0	146.4
Nov. 7– 8	100.6	27.9	128.5	91.6	23.1	114.7
Nov. 8– 9	59.4	15.6	75.0	93.3	21.6	114.9
Nov. 9–10	94.5	13.6	108.1	80.0	6.5	86.5
Nov. 10–11	80.0	7.7	87.7	86.0	14.3	100.3
Nov. 11–12	49.3	6.4	55.7	71.3	4.7	76.0
Nov. 12–13	73.4	6.1	79.5	[3] 47.8	14.3	62.1
Nov. 13–14	66.5	11.2	77.7	54.5	1.6	56.1
Nov. 14–15	72.0	7.1	79.1	.....	.....	.....
Total	694.7	142.8	837.5	623.9	133.1	757.0
1923						
Nov. 5– 6	87.0	(63.4)	150.4	81.0	(63.2)	144.2
Nov. 6– 7	95.4	(38.3)	133.7	91.7	(28.6)	120.3
Nov. 7– 8	78.1	(18.4)	96.5	80.5	(13.9)	94.4
Nov. 8– 9	63.6	(11.3)	74.9	73.3	(15.7)	89.0
Total	324.1	(131.4)	455.5	326.5	(121.4)	447.9
1924						
Mar. 3–[4]4	15.6	20.3	35.9	18.8	[5] (19.7)	38.5
Mar. 4– 5	[6] 102.9	[6] 34.0	[6] 136.9	31.2	[5] (16.5)	47.7
Mar. 5– 6				34.1	14.4	48.5
Mar. 6– 7				35.8	5.5	41.3
Mar. 7– 8	40.2	6.5	46.7	51.2	[7] (8.9)	60.1
Mar. 8– 9	37.3	1.1	38.4	42.5	[7] (3.5)	46.0
Mar. 9–10	40.4	4.8	45.2	45.4	4.9	50.3
Mar. 10–11	38.7	3.9	42.6	37.1	6.0	43.1
Mar. 11–12	39.0	2.3	41.3	41.1	3.6	44.7
Mar. 12–13	29.7	[8] 0.0	29.7	.....	.....	.....
Total	343.8	72.9	416.7	337.2	83.0	420.2

[1] Values in parentheses are based upon analyses of composite samples; all others are based upon daily samples.

[2] Some urine lost; amount not known.

[3] About 200 gm. urine lost.

[4] Mar. 3–4 represents a 17-hour period from 2 p. m., Mar. 3, to 7 a. m., Mar. 4; all other days in this fast begin and end at 7 a. m.

[5] Based on composite sample for Mar. 3 to 5.

[6] Data for Mar. 4 to 7 combined, because analyses of urine and feces were not made in exact 24-hour periods during this time.

[7] Based on a composite sample for Mar. 7 to 9.

[8] There were no defecations between 7 a. m., Mar. 12, and 7 a. m., Mar. 13, but 0.62 kg. feces were passed between 7^h 10^m and 10^h 25^m a. m., Mar. 13, before the steer was fed; nitrogen content 2.38 gm.

as creatinine the higher is the nitrogen-level. Steers E and F were on an appreciably higher plane in this regard than were steers C and D. On the other hand, the creatinine coefficient may be taken as an indication of the reserve material, that is, as an indication of whether the animal is fat or lean, because the fatter the animal the lower will be this coefficient. Although it is in the realm of speculation, one may surmise that the appearance of creatine may be taken as an indication of the inability to utilize the store of fat on hand or the lack of fat of an adequate chemical composition.

NITROGEN LOSS

TOTAL NITROGEN EXCRETED IN URINE PER DAY AND DURING THE ENTIRE FAST

From the physiological standpoint, the interest in the chemical composition of the urine at the present day far exceeds that in the urinary nitrogen loss, which for years served as the only chemical index of protein disintegration. The chemistry of the urine, however, deals for the most part with the nature of the substances analyzed and their relative proportions in the urine, and the total urinary nitrogen still remains the best index of the total protein disintegration. Hence special consideration was given to the total nitrogen excreted in the urine in relation to the previous state of nutrition, the length of the fast, and the age of the animal. The total nitrogen was determined in the weights of urine shown in Table 27 (p. 100), secured in the conventional 24-hour periods. As pointed out in the discussion of this table, however, these weights do not represent exactly the urine excreted for 24 hours, but simply the actual voidings occurring between the beginning of the experimental day and approximately 24 hours from that time. In the discussion of the chemistry of the urine this inequality in time is in large part compensated by referring all the urinary excretions to the per hour basis, but for the purpose of studying the protein disintegration it seems best to consider the total urinary nitrogen excretion in 24 hours, notwithstanding the defect in the 24-hour separation and collection.

The 24-hour amounts of nitrogen excreted in the urine have therefore been given in Tables 31 and 32 for each day of the long fasts as well as the average 24-hour values for the preceding feed-periods. (See also Tables 28, and 29, pp. 108 and 111, for details of exact duration of the period of collection.) The data for the feeding-periods are separated from those for the fasting-periods by horizontal rules.

TABLE 32.—*Total nitrogen losses of steers E and F during fast in February 1924*

Date	Steer E			Steer F		
	Nitrogen in urine	Nitrogen in feces[1]	Total nitrogen loss	Nitrogen in urine	Nitrogen in feces[1]	Total nitrogen loss
1924	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
Feb. 11–12	19.8	.....	.....	20.6	.....	.....
Feb. 12–13	13.8	(11.4)	25.2	[2] 10.8	(15.4)	26.2
Feb. 13–14	24.6	(13.1)	37.7	20.2	(8.5)	28.7
Feb. 14–15	22.2	(7.4)	29.6	22.2	(8.9)	31.1
Feb. 15–16	36.4	(3.9)	40.3	32.0	(4.9)	36.9
Feb. 16–17	26.6	(1.6)	28.2	35.5	(2.7)	38.2
Feb. 17–18	.....	.....	.....	32.0	(1.9)	33.9
Total	123.6	(37.4)	161.0	152.7	(42.3)	195.0

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[1] Based on analysis of composite sample for Feb. 12 to 18. In the case of steer E this sample included the feces passed on the first day on feed after the fast.

[2] About 10 ounces of urine lost during the day.

Prior to the fasts, the average daily excretion of urinary nitrogen by steers C and D in the feed periods other than at the submaintenance level varied from 57.5 to 101.5 gm. Inasmuch as both animals received exactly the same treatment, the variations are much the same with both. The lowest value during the feed periods occurred prior to the fast in December 1921, and the highest prior to the fast in January 1922. In the pasture periods nitrogen determinations were not feasible. On March 2–3, at the submaintenance level prior to the fast in March 1924, a low amount of 30 gm. was observed on the average with each animal.

The total loss of nitrogen from the body during a fast will in all probability be determined in large measure by the level of the nitrogen metabolism at the start of the experiment. In those experiments following prolonged undernutrition it has been noted with man that an appreciable part of the body nitrogen may be lost as a result of undernutrition; in other words, there is a continuous negative balance. When a fast is started at a low nitrogen-level, obviously the drafts due specifically to the fast are less than when the fast is started at a higher level. Emphasis in the following discussion is therefore laid upon the fasts which followed maintenance feeding.

On the first day of fasting following maintenance feeding there was in all cases but one an increase in the urinary nitrogen of steers C and D as compared with the average value before the fast. In the fast in December 1921, steer D, however, actually excreted 8 gm. less. The increase was very large with steer C in the January 1922 fast, amounting to nearly 30 grams. Until the third day the 24-hour nitrogen excretion remained fairly constant, but usually decreased rapidly after the third day. In the discussion of the chemistry of the urine it was pointed out (see p. 115) that the minimum nitrogen excretion of steers C and D was not far from 40 grams per 24 hours. This excretion corresponds essentially to that of man on a nitrogen-free diet. The constancy in the daily amounts in the last part of each fast is striking.

The total amount of nitrogen lost from the body in the urine during each of these different fasts is likewise recorded in Tables 31 and 32. Naturally the larger amounts were lost during the longer fasts, and it can be seen that the 14-day fast made a considerable draft upon the protein store of steers C and D. On the assumption that each gram of urinary nitrogen lost from the body represents 6.25 gm. of dry protein (the conventional factor), the maximum draft upon dry protein was 4.84 kg. in the case of steer C and 4.73 kg. in the case of steer D. In both instances, as is to be expected, this maximum draft occurred in the 14-day fast. Multiplication of the amount of dry protein by the factor commonly used for the conversion of protein to flesh, i. e., 4.0, shows that steer C lost 19.4 kg. of flesh and steer D lost 18.9 kg. This method of computation follows the older usage of ascribing the entire urinary nitrogen loss to muscle-tissue, and although this method is obviously incorrect, it gives a hint as to the actual weight of nitrogen lost in the breakdown of protein. Since chemical analyses of the bodies of these animals were not made, a computation of the percentage loss of total protein is hardly significant, owing to the variations in the proportion of protein in the body and particularly to the fact that these animals were subjected to numerous intermittent fasts and were on various feed levels. It can be seen, however, that there was a substantial draft upon the body-tissue during the 14-day fast.

Total Nitrogen Loss During Fasts of 5 to 14 Days

Although the nitrogen in the urine particularly represents protein metabolism and the nitrogen in the feces supposedly unabsorbed nitrogen of food, we have already seen (p. 123) that in the urine at least hippuric-acid nitrogen and amino-acid nitrogen may not represent protein disintegration, but simply a path for the excretion of food nitrogen, which has actually not been metabolized. Similarly, it is not inconceivable that certain nitrogenous products in the feces, formerly grouped under the general head of "metabolic fecal nitrogen," may in the case of humans represent actual metabolic transformations. With these reservations it may be maintained that the nitrogen of urine represents the disintegration of protein, and the nitrogen of feces unabsorbed feed nitrogen. Considering the animal at the beginning of the fast as a unit consisting of its organized body-tissue plus the contents of its intestinal tract, one may note the total loss of nitrogen from this unit during the period of fasting by summing the nitrogen lost in the urine and that lost in the feces, without attempting to differentiate between the urinary and fecal nitrogen on the basis of metabolized or non-metabolized nitrogen. Such computations have likewise been recorded in Tables 31 and 32.

During the fasts in December 1921, November 1923, and February 1924, the fecal nitrogen was determined only for the entire period of the fast and the amount of nitrogen has been apportioned between the different days upon the basis of the fresh weight of feces passed daily, on the assumption that the percentage of nitrogen in each day's feces was the same throughout the entire fasting-period. This assumption is probably not justified, although in lieu of daily nitrogen determinations it may be used here tentatively. The same treatment has been given to the data for fecal and urinary nitrogen in the feed-periods preceding the fasts, and to certain data in the fasts in March 1924. The values thus computed have been inclosed in parentheses. The nitrogen loss due to epidermal tissue and hair, which is a measurable amount, has not been estimated, although Armsby and, indeed, before him Grouven, took such loss into consideration.

In the fast in April 1922, steers C and D each lost over 900 grams of nitrogen. As is to be expected, the total loss varies again with the length of the fast and particularly with the character of the ration prior to the fast. Thus, since steers C and D had undergone a loss of nitrogen when receiving submaintenance rations prior to the fasts in March 1924, their total daily loss of nitrogen during these fasts averaged not far from 40 grams. Essentially the same loss was noted after the eighth day of fasting following maintenance feeding. During the fasts of steers E and F in February 1924, the total loss of nitrogen was approximately 30 grams per day with each steer, indicative not only of similar body-weights but likewise of the submaintenance level of nutrition.

Our data are wholly inadequate for the study of the recovery after fasting and the rapidity of nitrogen retention, as our main problem was the course of the metabolism during complete fasting. Substantial losses of nitrogen are experienced by steers when fasting, even when the normal nitrogen storage has been considerably depleted by the prolonged use of a submaintenance ration.

BODY MEASUREMENTS, GENERAL BODY CONDITIONS, AND PHYSIOLOGICAL FUNCTIONS

Body Measurements

General body measurements were taken before and after the fasts of five or more days' duration. In addition, three different body circumferences, namely, around the paunch, the flank, and the chest, were measured daily during the entire experimental season. The measurements obtained at the beginning and end of the fasts are of special interest, as they indicate whether any marked changes have occurred that might possibly have a significant correlation with loss of body-tissue and conceivably also with changes in body-surface area. As a typical illustration, the general body measurements secured at the beginning and end of the 14-day fast in April 1922 are recorded in Table 33. Since this was the longest fast, these data will obviously indicate the maximum variations noted in the size of the measurements due to fasting.

The only body measurements which show a significantly large decrease during fasting are the circumferences of the middle part of the body, sometimes termed the "barrel." In the order of magnitude the shrinkage is greatest at the paunch, slightly less at the flank, and materially less at the chest. In other words, the shrinkage at paunch and flank reflects largely the loss in fill, the chest circumference being but slightly affected by this loss. These measurements are therefore of value chiefly because they might conceivably be used as a crude basis for estimating the change in surface area. The body-length changes but little. Since it is evidently one of the dimensions which furnish fairly distinct landmarks for repeated measurements, it may prove a useful measurement in connection with some of the more recent formulas for determining surface area. The other dimensional measurements have no particular value as indicators of shrinkage during fasts not exceeding 14 days in length, because for the most part it is difficult to obtain duplicate readings successively, the error introduced thereby often exceeding the most probable actual change. They are valuable only in giving a general idea of the size and proportions of conformation of the animal.

Special emphasis was laid upon the measurement of the chest-girth, for it had been noted in an earlier study of undernutrition in steers that the chest-girth was influenced the least by changes in fill and that a change in this girth more truly represented an actual alteration in the state of flesh. Hence changes in chest circumference are of far more significance quantitatively than changes in body-weight. Obviously, in making this measurement, care must be taken to have the traction on the measuring tape or chain uniform, and it is preferable to have the same observer make the measurements from day to day, to insure both the uniform traction and the exact location of the tape.

TABLE 33.—*General body measurements at the beginning and end of the 14-day fast*

Measurement	Steer C			Steer D		
	Start	End	Difference	Start	End	Difference
Body circumferences:	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*
Chest	198.0	193.0	5.0	208.5	200.5	8.0
Paunch	228.5	200.5	28.0	228.5	208.5	20.0
Flank (rear)	198.0	172.0	26.0	200.5	183.0	17.5
Chest width	52.5	47.0	5.5	53.0	50.0	3.0
Chest depth	75.0	72.0	3.0	79.0	79.0	0.0
Width at hips	57.0	54.5	2.5	62.5	58.0	4.5
Body length[1]	160.0	157.5	2.5	165.0	162.5	2.5
Fore leg length	82.0	77.5	4.5	84.5	83.0	1.5
Hind leg length	96.0	95.0	1.0	99.0	99.0	0.0

[1] Measurement from second dorsal vertebra to pin-bone.

The measurements of the chest circumference secured during the fasting experiments of 5 to 14 days are recorded in Table 34, and, for purposes of comparison, the measurements secured on the three food days just prior to the fasts are also given. It can be seen that the normal variation in this measurement to be expected from day to day during feeding usually is not far from 2 to 3 cm., although before the April fast of steer C and the December fast of steer D a variation of 4 cm. was noted. Shortly after the beginning of the fast there is a decrease in the chest-girth, and this decrease continues as the fast progresses, although it is by no means uniform. Thus, in the 14-day fast, the chest circumference of steer C decreased from 198 cm. at the start to 193 cm. at the end, that is, there was a total shrinkage of 5 cm. Steer D, in the corresponding fast, lost 9 cm. On the other hand, in the fast after pasture in November 1922, the chest circumference of steer C decreased from 211 to 203 cm., a change of 8 cm. With the young animals which fasted not over four to five days after submaintenance feeding, the changes in chest circumference were hardly outside the range of the normal error of observation. Therefore, although, theoretically at least, the chest circumference should be a fairly good index of the state of nutrition and the loss of flesh, practically it serves only as a general index and can not be considered as a quantitative index, even in a fast of from 10 to 14 days.

Each of the entries in this table represents the chest circumference at the beginning of the day. Records were also made at the end of the last fasting day. These, with one exception, show either no change or a decrease of only 1 cm. as compared with the circumference at the beginning of the last day. At the end of the January fast of steer D there was a decrease of 3 cm., from 206 to 203 cm. Thus there was no measurable loss during the last day of fasting.

The experience in using the chest circumferences in the earlier study of undernutrition in steers had led to the belief that this was an important

TABLE 34.—*Chest circumferences prior to and during fasts of 5 to 14 days*[1]

Steer and dates of fasts	Days before fast			Days fasting													
	3	2	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Steer C:	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*
Dec. 6 to 13, 1921....	201	201	202	201	201	201	198	198	196	.....	.....	.....	.....	.....	.....	.....	.....
Jan. 4 14, 1922....	199	.....	198	198	198	196	196	196	194	194	196	193	193	.....	.....	.....	.....
Apr. 17 May 1, 1922.	202	201	198	198	199	198	196	197	196	196	196	196	194	194	193	193	193
June 1 7, 1922....	199	201	199	198	198	197	196	193	193	.....	.....	.....	.....	.....	.....	.....	.....
Nov. 6 16, 1922....	.....	.....	.....	.....	211	211	211	208	206	206	203	203	.....	.....	.....	.....	.....
Nov. 4 10, 1923....	.....	.....	.....	.....	216	216	213	213	212	.....	.....	.....	.....	.....	.....	.....	.....
Mar. 3 13, 1924....	207	208	208	208	206	203	203	203	203	203	203	202	203	.....	.....	.....	.....
Steer D:																	
Dec. 6 to 13, 1921....	208	208	212	212	208	206	206	206	206	.....	.....	.....	.....	.....	.....	.....	.....
Jan. 4 14, 1922....	206	.....	208	211	208	208	206	206	206	206	203	206	206	.....	.....	.....	.....
Apr. 17 May 1, 1922.	208	208	208	210	206	206	203	203	203	203	203	202	202	203	203	201	201
June 1 6, 1922....	206	206	206	206	203	205	203	201	.....	.....	.....	.....	.....	.....	.....	.....	.....
Nov. 6 14, 1922....	.....	.....	.....	.....	213	213	213	211	211	211	.....	.....	.....	.....	.....	.....	.....
Nov. 4 9, 1923....	.....	.....	.....	.....	218	216	216	216	.....	.....	.....	.....	.....	.....	.....	.....	.....
Mar. 3 12, 1924....	211	213	213	211	213	211	211	211	208	208	211	208	.....	.....	.....	.....	.....
Steer E:																	
Feb. 12 to 17, 1924....	138	138	140	140	140	140	137	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Steer F:																	
Feb. 12 to 18, 1924.....	145	146	145	147	147	145	145	145	.....	.....	.....	.....	.....	.....	.....	.....	.....

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[1] The chest circumferences of steers C and D were measured at 2 p. m., those of steers E and F at 7^{h}30^m a. m. As recorded in this table, they represent measurements secured at the *beginning* of each day.

physical measurement, which would give an index of the state of nutrition of the animals. It is much to be regretted that a good index of the state of nutrition comparable to the numerous indices of state of nutrition now available for humans is not yet available for animals. The personal equation of the experienced judge will still have to be allowed to enter into every estimate made, until a series of girths or lengths or ratios to weight can be agreed upon by the majority of livestock judges, which will possibly put this important estimate upon a mathematical basis. Such experience as is outlined in Table 34, however, is disconcerting, and it is clear that one measurement alone may not be considered as appropriate for such an index. No attempt has been made to combine this measurement with lengths or with weights or with any functions of body-weight, since the quantitative expression of the state of nutrition of animals is still unsettled.

GENERAL BODY CONDITIONS

During each of the fasts a daily record was kept of all incidents relating to the general appearance and behavior of the fasting animal, and particular note was made of such reactions as could not be measured or expressed in terms of concrete data. These observations are summarized under two heads, the effect of fasting on general behavior and the effect of fasting on physical appearance.

GENERAL BEHAVIOR OF FASTING STEERS

With humans, particularly in the lay mind, the idea of fasting is always inseparably interwoven with food shortage under enforced conditions, and it therefore implies hardships and suffering. In animals the actual sensations, if any, resulting from lack of food are not obscured by the capacity to reason, and their general behavior is therefore more truly an expression of the physical sense of uneasiness resulting from lack of food. In a study of steers during prolonged undernutrition[a] it was found that when the ration was reduced from a maintenance ration to one about half sufficient for maintenance, the steers showed some nervous irritation for a few days, after which those on submaintenance showed no more eagerness for food than did the steers which were still on full rations. The general deduction is that the so-called "hunger feeling" is merely the temporary sensation caused by the physical contraction of the alimentary tract to meet the requirements of a diminished bulk, but in no sense represents distress due to a lack of nourishment to the tissues.

Disposition and behavior—During the fasting experiments there was always some protest from the animals when the first feed was withheld. This was made manifest by a continuation of the usual signs which cattle exhibit at feeding-time. In other words, they were apprehensive and uneasy for several hours beyond the time when feed would normally have been given, at times lowing and showing general nervous irritation at being thus apparently neglected. As a rule, they behaved very quietly by the second day, showing no particular sign of uneasiness, irritation, or craving for food except after drinking, when at times they repeated their exertions

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 176.

up to the fifth or sixth day, although less and less persistently than on the first day. Their placid and indifferent attitude after the first day of fasting was, in fact, a surprise. On the whole, these fasting steers seemed to adjust themselves temperamentally to an entire lack of food even more readily than was the case with steers which were fed only half a maintenance ration. Previous to the beginning of the 14-day fast, when steers C and D were on a ration containing 9 kg. of hay and 3 kg. of meal (equal parts by weight of corn meal, linseed meal, and bran), they were very restless and acted anxious for food at meal time. On the afternoon of the first day, when their first meal was withheld, they exhibited this symptom to a marked extent. On the second day, although they still showed a tendency to nervousness from lack of food, they were somewhat more quiet and seemed to spend less time standing than when on feed. By the end of the second day they were very quiet and inactive and remained so during the rest of the fast, showing no particular irritation or craving for food.

Vigor—Loss in vigor due to prolonged undernutrition or to malnutrition in livestock is usually accompanied by a dull, listless expression. Brightness of eye and of general expression, on the other hand, is ordinarily considered a characteristic mark of vigor and particularly of good health. If these commonly accepted expressions have any basis of fact, then a dull, listless expression may be considered as a danger signal, suggesting that health is being impaired or undermined. In no case of fasting did any of these steers show any signs of a lack of vigor, judged on this basis. At the end of the 10-day fast in January 1922, steers C and D were apparently as vigorous as on the third day, and even at the end of the 14-day fast they were still as active and alert as ever, when taken outdoors to be photographed. Both animals stood up for much shorter intervals as the fasts progressed, but they seemed to rise with apparent ease, showing no particular weakness in this respect, even at the end of the 14-day fast. During this fast they did, however, relax more on going down, performing the last part of the operation with more or less of a drop, due no doubt in part to the fact that they had been confined in stalls for about 5 months and were somewhat stiff from lack of exercise. In general, they both appeared as strong and vigorous, even on the last day of the 14-day fast, as in the early stages of fasting, their eyes being bright, indicating that health or vigor had been in no wise impaired.

Muscular activity—The close correlation between muscular activity and metabolism, observed so frequently with humans and likewise pointed out with animals, made direct comparative records of muscular activity an essential part of our technique. With stall-fed steers, practically the only pronounced activity is that of getting up and lying down. These changes of position were indicated in the laboratory room by means of a small weight attached to one end of a cord running over pulleys, the other end being attached to the urine harness, so that, when the animal stood up, it would be instantly indicated and the time could be recorded. Time records of these changes of position were kept throughout the day, and in fasting experiments throughout the night also. These records give information not only of the number of changes from standing to lying and vice versa, but likewise of the total amount of time in the 24 hours that the animals were, respectively, standing or lying. The records are not complete, however, with regard to this latter phase of the observations, for such records involve continuous observations for 24 hours throughout the entire fast, and the pressure of other work occasionally introduced lapses in these records. The general picture, however, indicates that the animals had a tendency to lie down for a longer time as the fast progressed. Indeed, in all cases the fasting steers exhibited the same tendency to conservation of energy as was noted with the steers on undernutrition. They became more quiet and inert in their muscular exertion and spent a larger proportion of the time lying down and for much longer periods at a time than when on feed. Armsby and his associates have been wont to compute the 24-hour metabolism of their animals on the basis that the animal spent 12 hours standing and 12 hours lying. These times represent the average times presumably with animals on feed. These fasting steers, however, more commonly spent 14 to 15 hours instead of 12 hours in the lying position. Minor muscular activities also affect the metabolism considerably. In the respiration chamber such minor muscular activity was graphically recorded by means of the kymograph.[a] The kymograph records show conclusively that the degree of activity decreased as the fast progressed. The activity for the most part consisted in a shifting in the weight of the animal's position, usually with a remarkable degree of regularity. The time elapsing between these shifts in weight gradually lengthened as the fast progressed. In the long fast of 14 days steer D invariably showed a somewhat greater activity than steer C. There was not much difference in the number of times that the animals stood up and lay down, i. e., the actual number of times that they shifted their position was not greatly altered, but they remained down for a longer time.

Salivation—After the second day of fasting, steer D almost invariably began salivation, sometimes rather profusely, and continued to salivate up to the fifth day, but the salivation had gradually ceased by the seventh day. The fact that none of the other three fasting steers ever exhibited this trait showed that this was an individual characteristic. Obviously the salivation of steer D was somehow associated with lack of food, but the absence of other manifestations suggesting a craving for food implied that the salivation was probably induced in part by the condition of his teeth, as is so commonly the case in horses.

Rumination—After the second day rumination practically ceased, although there were occasional evidences of it. For example, no rumination was recorded after the fourth day, except in the 10-day fast in January, when steer D apparently showed evidences of rumination. On the whole, rumination persisted somewhat longer during fasts following feeding with dry rations, having hay for a basis, than it did during fasts after grass feeding. This would naturally be expected, as it would probably take a longer time to saturate and prepare hay thoroughly for rumination.

Behavior during refeeding after fast—Close observation of the behavior during the refeeding period after the fast thoroughly corroborates the

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[a] **Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 54.**

deductions drawn from their behavior during fasting. Frequently only hay was given for the first feed, on the assumption that it would be better at the start to supply bulk rather than highly concentrated matter. When the first hay feed was given after a fast of 5 or more days, the steers consumed the feed in an indifferent manner, eating intermittently and slowly, showing no signs of avidity or eagerness, as one might suppose. After these longer fasts their capacity or desire for any material amount of bulk in the form of hay was apparently limited, as they usually consumed less than 2 kg. in their first feed and, when only hay was fed, from 4 to 7 days would elapse before they would again clean up a ration of hay approximating normal maintenance. In those cases where 1,000 grams of a concentrated meal mixture (equal parts by weight of linseed meal, corn meal, and wheat bran) were given, the meal was cleaned up in 15 minutes, which was still a much longer time than the steers required for this amount under ordinary conditions of feeding. When the animals were refed on both hay and meal, their appearance would improve within 2 or 3 days, as the paunch again became distended and the hair smoothed down. Likewise they would become more energetic, and in a week or less they would behave and appear much the same as before the fast.

General Appearance

In all fasts the first visible effect of the lack of food is the shrinking of the body at the paunch. In the fasts of from 2 to 5 days this shrinking in size was confined largely to the region of the paunch, but toward the end of the two 10-day and the two 14-day fasts a pronounced shrinking or sinking in at the flanks also became apparent. The shrinkage at the paunch was most marked during the first 2 or 3 days, corresponding closely to the quantitative rate in loss of solid excreta and water of fill. After the fasts which did not exceed 5 to 7 days in length, this shrinking in the size of the body apparently was repaired within a week, when the animals had again acquired the capacity to consume a full ration of hay and a normal complement of water.

Condition of flesh—Nothing is so important to the experienced stockman in estimating the state of flesh of an animal as is visual appraisal. Weight, length, or girth does not so perfectly express to him the true condition of flesh of the animal. Such personal appraisal was, however, in the case of these steers, supplemented by standard measurements of lengths and girths. As a result of the fasts of these four animals there was no visible indication of any loss in flesh, even after the 10-day and the 14-day fasts, the thighs and hind quarters generally appearing as plump as before the fast. This impression was also obtained from "handling"[a] or feeling the flesh over the ribs, a butcher's procedure. Although both steers C and D were extremely gaunt at the end of the 10-day and the 14-day fasts, Professor McNutt, of the Department of Animal Husbandry of New Hampshire College, commented on their appearance as follows:

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[a] "Handling" is a general expression used by butchers and livestock men generally to indicate thickness and quality of flesh.

"The steers are in good condition, considering the length of the fast. They have apparently lost very little flesh and still handle well, but they have undergone considerable shrinkage due to loss of fill. I have seen cattle undergo greater shrinkage in a 3-day shipment on cars than these two steers show."

Skin and hair—When animals in good flesh are well nourished, as was the case previous to all but those fasts following submaintenance feeding, the hair is soft, fairly glossy, and lies flat on the body, giving the impression of sleekness. The skin is soft, pliant, and elastic to the touch or manipulation. Close daily observation and handling or feeling of skin and hair throughout each fast indicated that the hair was particularly sensitive to radical changes in food-supply, reacting much more quickly to lack of nourishment than was true of the skin. Usually by the second or third day of fasting the hair began to lose its sleekness and bristled out more from the body, having a dusty appearance, and after 10 or more days of fasting it became somewhat harsh or dry to the touch.[a] During the 10-day and the 14-day fasts considerable shedding also took place, but since both of these fasts occurred during the spring of the year, the cause must have been at least partially seasonal. No particular effect on the skin was observable, even after 5 days of fasting, but at the end of the 10-day and 14-day fasts, probably because of a lack of replacement of fat in and more particularly under it, the skin seemed to become drier and harder and consequently to shrink, so that it adhered more tightly.

HEART-RATE

The heart-rate is a reasonably good index of the general metabolic level. Extraordinarily low rates have been previously reported for steers on submaintenance rations,[b] 20 beats per minute being noted in the case of one steer. Since simultaneously with the low heart-rate there was a greatly lowered "standard metabolism" (see p. 228), it can be seen that with these animals, as with humans, variations in heart-rate reflect approximately, at least, the metabolic level. The importance of recording heart-rates in studies with steers is here strongly emphasized, as this relationship between heart-rate and metabolic activity is so prominent. The technique, however, is by no means simple. Accurate determinations of representative heart-rates, as well as live weights, can be secured only with the greatest patience and care. They should be obtained by a regular attendant and under conditions when the animal is placid or quiet and has not been unduly excited. The animal should also not be ruminating throughout the entire time of counting the heart-rate, since rumination increases heart activity. The best results so far have been obtained by use of a stethoscope placed over the heart of the animal. It is not at all unlikely that electrocardiograms might be secured by attaching simple, wet electrodes to the legs, making the electrodes a part of the regular harness. Such an arrangement would be ideal and probably would give much more normal, uncom-

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[a] The appearance of these changes depends of course on the physical conditions in which the animals start fasting.

[b] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 193.

TABLE 35.—*Heart-rates per minute of steers C and D, on feed and fasting*

Date	Days fasting	Steer C			Steer D		
		2 p. m.	4 p. m.	6 to $7^{h}30^{m}$ a. m.	2 p. m.	4 p. m.	6 to $7^{h}30^{m}$ a. m.
1921							
Dec. 3 to 5, incl.	....	49	52	42	52	55	51
Dec. 6– 7	1	[1]44	[1]40	44	[1]44	48	48
Dec. 7– 8	2	....	[1]32	36	....	[1]36	36
Dec. 8– 9	3	32	36	34	36	32	40
Dec. 9–10	4	32	[1]32	....	36	42	....
Dec. 10–11	5	38	36	....	38	42	....
1922							
Jan. 1 to 3, incl.	....	68	61	60	70	63	64
Jan. 4– 5	1	[1]64	[2]72	[1]48	[1]72	[2]68	[1]52
Jan. 5– 6	2	48	60	[1]38	48	[1]48	[1]40
Jan. 6– 7	3	[1]36	[1]36	[1]38	[1]40	40	[1]36
Jan. 7– 8	4	36	[1]36	[1]36	40	40	[1]38
Jan. 8– 9	5	40	[1]36	[1]38	[1]38	[1]36	[1]36
Jan. 9–10	6	34	[1]32	38	[1]36	[1]38	36
Jan. 10–11	7	[1]30	32	36	[1]32	[1]36	38
Jan. 11–12	8	[1]32	[1]28	[1]30	36	32	38
Jan. 12–13	9	36	[1]28	34	36	30	[1]36
Jan. 13–14	10	[1]28	28	38	[1]28	[1]34	[1]27
Apr. 14 to 16, incl.	....	57	56	51	60	61	60
Apr. 17–18	1	....	60	42	[1]62	54	50
Apr. 18–19	2	42	52	38	[1]40	....	36
Apr. 19–20	3	36	[1]32	38	[1]36	....	40
Apr. 20–21	4	[1]32	[1]30	38	[1]34	....	40
Apr. 21–22	5	38	36	34	42	....	30
Apr. 22–23	6	37	[1]32	30	42	....	38
Apr. 23–24	7	36	34	30	40	36	30
Apr. 24–25	8	[3]40	36	32	36	40	[1]34
Apr. 25–26	9	30	[1]30	34	38	[1]32	[1]38
Apr. 26–27	10	[3]44	[1]36	[1]32	40	48	[1]36
Apr. 27–28	11	32	36	[1]30	40	32	[1]32
Apr. 28–29	12	30	32	32	[3]36	38	[1]32
Apr. 29–30	13	[3]38	[1]28	32	32	....	34
Apr. 30–May 1	14	30	[1]34	30	32	[1]34	[1]32
May 29 to 31, incl.	....	63	61	55	71	68	65
June 1– 2	1	[1]56	....	40	[1]64	60	54
June 2– 3	2	44	48	[1]40	54	....	[1]40
June 3– 4	3	[1]44	[2]44	[3]44	52	....	[3]48
June 4– 5	4	34	38	32	44	42	44
June 5– 6	5	38	[1]36	34	48	....	46
June 6– 7	6	48	[2]33	32	....	....	....
Nov. 6 to 7	1	....	....	[1]48	....	....	[1]48
Nov. 7– 8	2	44	40	[1]38	48	....	[1]40
Nov. 8– 9	3	40	[3]48	44	48	....	[3]52
Nov. 9–10	4	40	48	40	48	....	52
Nov. 10–11	5	40	38	40	[1]48	....	46
Nov. 11–12	6	[1]38	[1]36	[1]36	[1]44	....	[1]42
Nov. 12–13	7	36	38	36	46	42	40
Nov. 13–14	8	38	36	36	42	[1]38	40
Nov. 14–15	9	[1]36	[1]34	38	....	....	....
Nov. 15–16	10	36	40	36	....	....	....

[1] Lying. [2] Lying and ruminating. [3] Just up.

TABLE 35.—*Heart-rates per minute of steers C and D, on feed and fasting*—Continued

Date	Days fasting	Steer C			Steer D		
		2 p. m.	4 p. m.	6 to 7^h30^m a. m.	2 p. m.	4 p. m.	6 to 7^h30^m a. m.
1923							
Nov. 1 to 3, incl.	....	....	61	....	....	69	....
Nov. 4– 5	1	....	....	[4] 52	....	....	....
Nov. 5– 6	2	....	....	48	....	....	60
Nov. 6– 7	3	46	48	44	72	....	52
Nov. 7– 8	4	[1] 36	42	[3] 48	[1] 56	....	[3] 56
Nov. 8– 9	5	[1] 36	42	[3] 40	52	....	[3] 56
Nov. 9–10	6	36	36	[1] 34	....	....	....
1924							
Feb. 29 to Mar. 2, incl.	....	35	37	35	46	49	46
Mar. 3– 4	1	34	34	36	48	48	48
Mar. 4– 5	2	32	30	30	44	....	36
Mar. 5– 6	3	[1] 26	28	[3] 40	[1] 32	36	36
Mar. 6– 7	4	28	26	[1] 28	32	34	36
Mar. 7– 8	5	26	[1] 24	28	36	48	[3] 48
Mar. 8– 9	6	[1] 26	[1] 30	[1] 24	....	[1] 40	[1] 36
Mar. 9–10	7	30	30	25	[3] 50	[1] 32	[1] 38
Mar. 10–11	8	[1] 26	26	[1] 28	....	34	[1] 36
Mar. 11–12	9	....	28	[1] 24	....	30	34
Mar. 12–13	10	[1] 26	[1] 26	34	....	....	....

[1] Lying. [3] Just up. [4] Taken at 8^h30^m a. m.

plicated results, but this method has not as yet been tested. Owing to the much disputed quantitative differences between the metabolism of an animal in the lying and standing positions, heart-rates recorded under these conditions should be studied more thoroughly. Certain technical difficulties in securing the heart-rate with the animal in the lying position are not easily overcome, but probably electrocardiograms under these conditions will be of much assistance in throwing light on this problem.

Colin[a] states that the average heart-rate of the steer is from 45 to 50 beats per minute, as shown by a large number of observations by veterinarians. Knoll,[b] in Ellenberger's laboratory at Dresden, found that the heart-rate of these animals varied between 36 and 102 beats per minute, being on the average 70 beats.

In connection with the fasts of 5 to 14 days the heart-rates per minute of all four of our steers were determined on most of the fasting days and in the feeding-periods preceding the fasts. Usually they were determined at 2 p. m., 4 p. m., and some time between 6 and 7^h 30^m a. m. The data secured on each of the fasting days, together with the average values for 3 days on food preceding each fast, are recorded in Tables 35 and 36. In these tables special note is made of the instances when the animal was lying, ruminating, or had just stood up at the time the heart-rate was

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[a] Colin, Traité de Physiologie Comparée des Animaux, 3d ed., Paris, 1888, 2, p. 476.

[b] Knoll, Untersuchungen über die normale Pulsfrequenz der Rinder und Schweine nebst vergleichenden physiologischen kritischen Studien über die normale Pulsfrequenz des Menschen und der Haussäugetiere. Inaug. Diss., Zurich, 1911, p. 40.

TABLE 36.—*Heart-rates per minute of steers E and F, on feed and fasting*

Date (1924)	Days fasting	Steer E			Steer F		
		2 p. m.	4 p. m.	7^h30^m a. m.	2 p. m.	4 p. m.	7^h30^m a. m.
Feb. 9 to 11, incl.	....	45	44	36	46	43	36
Feb. 12–13	1	38	42	40	48	44	48
Feb. 13–14	2	36	48	36	[1]40	44	36
Feb. 14–15	3	[2]34	36	34	36	36	36
Feb. 15–16	4	[2]34	[1]48	36	38	36	32
Feb. 16–17	5	34	[2]36	36	40	34	[2]34
Feb. 17–18	6	....	....	....	36	36	36

[1] Just up. [2] Lying.

observed, for such factors might have considerable influence on the heart-rate.

Attention is first called to the average heart-rates in the food-periods prior to the fasting experiments. In the case of steer C, in December 1921, heart-rates of 49, 52, and 42 were noted. In January 1922, about a month later, considerably higher rates of 68, 61, and 60 were found. In April 1922, the values are 57, 56, and 51, about intermediate between the December and January values. In May the rate has again risen to 63, 61, and 55, but the most striking change is during the submaintenance period in February, when the values were 35, 37, and 35. Essentially the same picture is shown with steer D, although his heart-rate tends in general to be slightly higher than that of steer C. Indeed, even on submaintenance rations his heart-rate is pronouncedly higher.

Fasting results in an almost continuous fall in the heart-rate, noticeable at practically all three times of observation. The minimum rate noted with steer C is 24 beats per minute, which was found on three different occasions in the fast following submaintenance feeding in March 1924. The minimum rate noted with steer D was, singularly enough, not during the fast following submaintenance feeding, but during the fast in January 1922, when it was 28 and 27 beats per minute on the last day. The minimum rates were usually noted when the animal was lying. In the longest fast, from April 14 to May 1, the heart-rates fall off so that they are almost half of what they were on the prefasting feed-level. In the fast at the submaintenance level the fall is pronounced with steer C, but by no means so sharply marked as with steer D.

In the fasting experiments with steers E and F, of 5 and 6 days respectively, the heart-rates of steer E prior to fasting were 45 beats per minute at 2 p. m., 44 beats at 4 p. m., and 36 beats at 7^h 30^m a. m. Almost exactly the same values were found with steer F. These animals began fasting after a long period on submaintenance rations. The minimum heart-rate of steer E was 34 beats, a rate which was noted at least four times toward the end of the fast. With steer F a low rate of 34 beats was also noted on two occasions, but the minimum rate was 32 beats at 7^h 30^m a. m. on the fourth day. The picture is essentially the same with both animals and is in conformity with the picture shown by steers C and D, that is, a distinct falling off in the heart-rate as the fasting progresses.

The relationship between the heart-rate and the metabolism, a relationship which has frequently been pointed out in earlier publications from the Nutrition Laboratory, is strikingly shown in the series of 4-day experiments with steers E and F in 1924–25. The heart-rate was not determined while the animal was inside the respiration chamber, but it was determined twice a day for at least a week prior to each respiration experiment. Thus, the heart-rate of steer E, when on a maintenance ration of 7 kg. of hay, either timothy or alfalfa, was not far from 46 to 54 beats per minute, the higher values being observed at the low environmental temperature and with the alfalfa hay. Preceding the submaintenance experiments with timothy hay, as low a value as 33 beats was found prior to January 13, 1925. The effect of the cold environmental temperature and submaintenance feeding on timothy hay prior to February 2, 1925, is reflected in a higher heart-rate of 41 beats, as compared to 33 beats in the earlier submaintenance experiment. When alfalfa hay was fed, the heart-rate fell from approximately 50 beats on the maintenance level to 32 beats on the submaintenance level.

With steer F the picture is almost identically the same. With the maintenance ration of timothy hay the heart-rate ranged from 45 to 50 beats per minute. On the submaintenance ration of timothy hay it was 34 to 35 beats. In both instances the environmental temperature was about 22° C. With a lower temperature and a submaintenance ration of timothy hay the heart-rate was a little higher, 42 beats. On the maintenance ration of alfalfa hay the rate was 46 to 52 beats and on the submaintenance ration of alfalfa hay it fell to 36 beats, although the environmental temperature remained the same, i. e., about 22° C. The state of nutrition evidently has a pronounced effect on the heart-rate, and there is a strong suggestion of a more rapid heart-rate with a lower environmental temperature.

RESPIRATION-RATE

The extremely high respiration-rates commonly noted in very fat animals suggested that records of the respiration-rate should be made a part of the daily observations, and accordingly during the winter of 1924 and 1925 an attempt was made to secure regular records of this important physiological factor. It was found even more difficult to secure reliable records of the rate of respiration than of the heart-beat. The extraneous gross movements of these ruminants are so frequent that a kymograph curve can not properly record the respirations for more than a few seconds at a time. It is practically impossible for any one other than the regular attendant to secure such data without extraordinary precautions, and care should be taken that the animal is not apprehensive, has undergone no physical exertion, and is not eating or ruminating at the time. The application of a pneumograph about the thorax as a part of the regular harness, a method so successfully used by Pott,[a] has not thus far been attempted in our research. We have attempted to count the respirations by watching

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[a] Pott, Ohio Journ. Sci., 1918, 18, p. 129.

the movements of the chest, and, in some instances, by placing the hand over the nostrils. The animals seemed to be extraordinarily susceptible to slight changes in environment, so that the respiration-rates can not be discussed except with greatest reserve. Exercising every care, but not employing the pneumograph, we secured a few observations during fasting days, and these are recorded in Table 37. The data are so few that discussion of them is hardly justified. It would appear, however, as if during fasting the respiration-rate of these animals was not far from 9 or 10 respirations per minute. It is obvious that much remains to be done in studying the respiration-rate of steers, and undoubtedly the pneumograph must replace any manual or visual counting.

TABLE 37.—*Respiration-rates of fasting steers*

Steer and date (1924)	Days fasting	Number of records	Respiration-rate per minute (average)
Steer C:			
Mar. 4	2	4	10
Mar. 5	3	5	11
Mar. 12	10	5	9
Steer D:			
Mar. 4	2	3	9
Mar. 11	9	2	9
Steer F:			
Feb. 17	6	2	9

RECTAL TEMPERATURE

The profound changes noted during fasting in the body-weight, the circulatory activity (as indicated by the heart-rate), and the general condition of the animal (as exhibited by the external appearance, and the decrease in metabolism and in muscular activity), all suggested that fasting might have an influence upon the rectal temperature. Hence, throughout the entire research, rectal temperatures were recorded at specific hours of the day (usually at 2 p. m., 4 p. m., and 6 or $7^h 30^m$ a. m.). A veterinarian's thermometer was used, and almost invariably the same observer made the readings, due precautions being taken as to the length of time that the thermometer was inserted and that the depth of insertion be 10 cm. With stall-fed animals the diurnal variation in temperature should be studied, preferably with a resistance thermometer or a thermo-electric element, and frequent observations should be made. Thus far, however, no attempt has been made to use such a technique.

Space will not permit of publishing the long series of observations which were secured on the rectal temperature of these steers. A careful examination of the data shows that the two animals, C and D, had almost invariably the same rectal temperature, which averaged not far from 38.2° C. In general, the highest temperatures were noted at 2 p. m. and the lowest at 6 a. m., suggesting a diurnal rhythm. During the fasts the rectal temperature on the average was but two or three tenths of a degree higher on the first day than on succeeding days, but after the second day remained reasonably uniform throughout the entire fast, irrespective of its length.

The highest rectal temperature observed during the fasting days was 39.2° C. on January 4, 1922, at 2 p. m., with both steers C and D. The lowest temperature observed was 37.2° C. This temperature was noted in a number of instances, namely, at 4 p. m., November 8, 1923, with steer C; at 7 a. m., November 9, 1923, with both steers C and D; and at 4 p. m., March 4, 1924, with steer C. The rectal temperature was essentially the same throughout all the fasts, irrespective of the previous state of nutrition or the character of the ration. Thus, in the fast following submaintenance feeding in March 1924, the rectal temperature was on the average only one-tenth of a degree lower than in the other fasts.

Steers E and F, during their fast in February 1924, following submaintenance feeding, had in general a slightly lower rectal temperature than steers C and D, the average temperatures ranging from 38.1° C. on the second day to 37.7° C. on the fifth day.

Examination of the data obtained on feeding days, to determine whether the different feed-levels and digestive activity possibly have an influence upon rectal temperature, indicates that the temperature was usually highest at 2 p. m., but in practically all cases the range in temperature was within 1° or 1.5° C. The barn temperature had a slight effect, for on the warmer days the rectal temperature was on the average one or two tenths of a degree higher than on the colder days. It would thus appear as if prolonged fasting resulted in no material disturbance of the normal rectal temperature, which was singularly unaffected either by changes in feed-level or by changes in environmental temperature.

Skin Temperature

The pronounced change in heat-production exhibited by these animals when fasting, and particularly following submaintenance rations, made a study of skin temperature of possible interest. During the March 1924 fast of steers C and D, which followed a submaintenance ration, the skin temperature was measured at six different positions on the body on the successive days of the fast. In these measurements the thermo-electric method was employed, which has been so extensively used with humans at the Nutrition Laboratory and which was used to a slight extent in the earlier research on undernutrition in steers.[a] The difficulty of securing the skin temperature of an animal whose skin is covered with hair has been pointed out frequently, but simply for purposes of comparison these measurements were made over the hair, that is, there was no attempt to place the thermo-junction at the base of the hair next to the skin. In an earlier research[a] the skin temperatures of 12 steers were noted on one day only. Unfortunately, the environmental temperature was not recorded, but the evidence was that it was high. With this high environmental temperature the average skin temperature of two groups of steers on submaintenance rations was not far from 32.4° C. In the fasting experiment of March 1924, the environmental temperature ranged from 14° to 18.5° C. The

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[a] Benedict, Miles, and Johnson, Proc. Nat. Acad. Sci., 1919, 5, p. 218; Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 75, 181, and 183.

average skin temperature of steer C was 27.5° C. and of steer D, 28.0° C. There was a slight tendency for the skin temperature to decrease as the fast progressed.

It is clear that the environmental temperature plays a large rôle in such studies, and that little can be stated until fasting experiments are made under uniform conditions of environmental temperature. No evidence is available as to what would have been the skin temperature of an animal on full feed at this environmental temperature. The fact that the average skin temperatures noted during this fast were nearly 4 or 5 degrees below those found in the earlier study on undernutrition is probably in large part accounted for by the difference in the environmental temperature, and it is reasonable to assume that the fasting *per se* or, indeed, the fasting and the previous submaintenance ration, were without material effect upon the skin temperature. This finding parallels in a general way the conclusion drawn with regard to the rectal temperature.

GASEOUS METABOLISM AND ENERGY RELATIONSHIPS

Metabolism Measurements Actually Made or Computed

As the best index of the total metabolic activity of a living organism physiologists have long accepted the heat-production and its accompanying gaseous metabolism, primarily the production of carbon dioxide and the absorption of oxygen. The apparatus at Durham, New Hampshire, was originally designed to measure only the carbon dioxide given off by the animal while inside the chamber. Subsequently the installation of the delicate gas-analysis apparatus designed by Carpenter (see p. 33) made possible the determination of the respiratory quotient, and from these two factors the actual oxygen consumption and the heat-production could be computed.

Methane—In the ruminant another gas enters into the gaseous metabolism, for as a consequence of the prolonged retention of food residues in the intestinal tract there are extensive fermentations which result in the production not only of material amounts of free carbon dioxide but of methane. In the case of humans and most carnivorous and omnivorous animals, methane is rarely present in measurable amounts and it is ordinarily disregarded in metabolism measurements. Since the study of the intestinal fermentation has given rise to the firm conviction that the methane production is an index of the digestive activity, the determination of methane has acquired new significance in metabolism measurements. In most of our earlier work methane determinations were impracticable. The extensive train of combustion furnaces and purifying devices formerly considered essential for such determinations were too complex for use with the apparatus installed at Durham, New Hampshire, as this apparatus was primarily designed for the simplest total metabolism measurement with ruminants, the idea being not to have it too complicated or elaborate for use by other experiment stations. On a visit of one of us to Copenhagen a device designed by Professor Møllgaard for the analysis and determination of methane seemed so promising that Dr. T. M. Carpenter, of the Nutrition

Laboratory staff, made a special visit to Professor Møllgaard's institute in the spring of 1925, and on his return to America he so modified his delicate gas-analysis apparatus (see p. 33) that we are now able to measure the methane production accurately. Up to the time of completing the collection of fasting data for this monograph, however, no determinations of methane had been made. Thanks to the kindly cooperative spirit of Professor Armsby in checking our first fasting experiment (which he helped to plan) by subsequently making two fasting experiments with cows, it seemed justifiable to proceed without these intricate determinations in our fasting experiments, because the methane investigations in Professor Armsby's laboratory indicated that during the first few days of fasting the formation of methane falls off rapidly.[a] It is of importance to note that in subsequent fasting experiments during the fall and winter of 1925–26 our methane data confirm fully the findings of Armsby and Braman, indicating that there is a rapid cessation of fermentative activity after the withdrawal of food. Our own determinations of methane will not be discussed in this monograph, however, as they do not apply to these particular fasting experiments. The value of methane measurements in the calculation of the energy transformations of ruminants has been pointed out by Andersen[b] and such measurements play an important rôle in his system of computing the heat-production from the measured oxygen consumption and carbon-dioxide production. This method of computing the heat-production has not been employed by us (see p. 148).

The close relationship between the carbon-dioxide production and the directly determined heat-production, early reported by Armsby and his associates, convinced us that the direct determination of the carbon-dioxide production alone would be of value in many problems of animal research, particularly when orientation is first desired. Stress was therefore laid upon the measurement of the carbon-dioxide production, and provisions were made for the accurate measurement of this factor in each experimental period of our research. This was the only factor determined quantitatively. The oxygen consumption was measured relatively by noting the carbon-dioxide increment and the oxygen decrement in the ventilating air-current, computing therefrom the respiratory quotient, and finally calculating the oxygen consumption from the respiratory quotient and the total carbon-dioxide production. It is thus seen that the most important measurement enabled by the apparatus at Durham, New Hampshire, is that of the carbon-dioxide production. During fasting experiments, particularly after the first day or two, the carbon-dioxide production is an accurate index of the actual heat-production. The reserve of carbohydrates in the food and body glycogen is heavily drawn upon during the first few days of fasting, and thereafter fat combustion predominates. The calorific value of carbon dioxide during fat combustion is essentially constant, and hence under fasting conditions this gaseous measurement of itself is an excellent index of energy transformations.

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[a] Details of these investigations Professor Armsby kindly submitted to us in correspondence, just prior to his untimely death. The data have subsequently been published by Braman, Journ. Biol. Chem., 1924, **60**, p. 85.

[b] Andersen, K. Vet. og. Landbohojsk. (Copenhagen), Aarsskr., 1920, p. 157; ibid., Biochem. Zeitschr., 1922, **130**, p. 143.

The relationship between the volume of carbon dioxide produced and the volume of oxygen consumed indicates the nature of the combustion in the body. When fats exclusively are burned, the respiratory quotient is approximately 0.70. Rarely is it found to be below this, and such quotients have been interpreted as indicating the possible conversion of fat into carbohydrate. When pure carbohydrates are burned, the ratio is 1.00, and it is usually assumed that a respiratory quotient above 1.00 indicates the transformation of carbohydrate into fat. With a combustion exclusively of carbohydrate the quotient of 1.00 is to be expected. If any carbohydrate is converted into fat, this results in an increased liberation of carbon dioxide and raises the quotient. It is highly improbable that there is a sharply defined line which separates a combustion exclusively of carbohydrate and the transformation of some carbohydrate into fat, even if the quotient does rise above 1.00. Thus, our colleague, Dr. T. M. Carpenter, is convinced, by his own experiences in gas analysis, that there may be a conversion of considerable carbohydrate into fat when the respiratory quotient is less than 1.00. Respiratory quotients over 1.00, however, have been commonly accepted as indicating fat formation and respiratory quotients of 1.00 or below as indicating carbohydrate combustion, the intensity of which depends upon the proportion of carbohydrate in the combustion, which becomes greater the nearer the respiratory quotient is to 1.00.

In lieu of direct calorimetric measurements (the apparatus at Durham not being designed to measure heat directly), it is necessary to calculate the heat-production from the gaseous exchange. The carbon-dioxide determination alone is of value, particularly when the heat factors of Armsby and his associates are used. The relationships between heat-production on the one hand, and carbon-dioxide production and oxygen consumption on the other hand, are well known. Thus, in the oxidation of the several organic substances which enter into the metabolism of the body, notably carbohydrates, proteins, and fats, the amount of heat liberated per liter of oxygen absorbed is relatively constant. The greatest variations in the calorific value of oxygen exist between the combustion of pure fat and the combustion of pure carbohydrates. With humans it has been found that 12 hours after the last meal, provided this has not been excessively rich in either carbohydrate or protein, the respiratory quotient on the average is 0.82. Under these conditions the oxygen absorbed has an energy equivalent of 4.825 calories per liter, and is an accurate measure of the energy transformations. With ruminants the case is not so simple. A respiratory quotient of 0.82 is rarely noted, except during the transition from regular feeding to a fasting condition. Usually ruminants are continually feeding and the quotient is generally 1.00 or slightly above. When feed is withheld for several days, the quotient rapidly falls to not far from 0.74 to 0.72. Under the feeding conditions the calorific value of oxygen represents a pure carbohydrate combustion, and under the fasting conditions almost a pure fat combustion. Between the two extremes there is a difference of about 6 per cent in the calorific value of a liter of oxygen. The corresponding difference in the calorific value of carbon dioxide is approximately 30 per cent. Hence the determination of the oxygen consumption *per se* places energy calculations upon a much more accurate footing.

Since our respiratory technique enabled the direct determination of the carbon-dioxide production and the respiratory quotient, it was possible to compute the heat-production either from the carbon-dioxide production or the computed oxygen consumption. From the actually determined heats of combustion of the various nutrients, such as proteins, fats, and carbohydrates, in the bomb calorimeter, and from a comparison of the measured energy and the carbon-dioxide production, it has been found that for each gram of carbon dioxide produced in the combustion of carbohydrate there is a production of 2.58 calories. On the contrary, when fat is burned, approximately 3.4 calories are produced for each gram of carbon dioxide. The difference between the two values makes it seemingly impossible to use carbon dioxide as an accurate measure of the heat-production of animals, except under conditions where the character of the combustion is fairly definitely known, as, for example, during prolonged fasting.

Due to the foresight of Professor H. P. Armsby,[a] however, a large number of measurements of the carbon-dioxide production and the heat-production of large ruminants in his calorimeter have been recorded, and the actual ratio between the carbon-dioxide production and the heat-production has been determined for different animals on various kinds and amounts of feed. Thus, it was at first thought that this relationship could be computed with a good degree of accuracy by the equation $Y_3 = -0.0226x + 2.802$, in which x is the air-dry weight of feed in grams per kilogram of live weight, and Y_3 is the measured heat-production per kilogram of live weight divided by the grams of carbon dioxide produced per kilogram of live weight.

These earlier experiments all dealt with animals which had been given varying amounts of feed. A subsequent series planned by Armsby included fasting experiments, and a revision of his earlier tabulations has been published by one of Armsby's associates, Braman,[b] who has suggested the modified equation $Y_3 = -0.02886\mathrm{x} + 2.883$. By using this equation, Braman has computed the heat-production from the carbon-dioxide production with a series of cows which had been fasting from 1 to 8 days. Obviously, in such instances the value of x is zero. The calculated heat-production is, however, invariably lower than that actually measured, and division of the observed heat-production by the observed carbon-dioxide production of these fasting cows shows that the calorific value of carbon dioxide, instead of being 2.883, is on the average nearer 3.105. In the first days of fasting, however, this value is somewhat different than in the later days.

For purposes of comparison of the heat-production as computed from the carbon-dioxide production and the actually determined respiratory quotient with the heat-production as computed from the carbon dioxide to heat ratio, we arbitrarily used the factor 3.02 as representing the calories per gram of carbon dioxide during the first 24 hours after food, the factor

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[a] Armsby, Fries, and Braman, Proc. Nat. Acad. Sci., 1920, **6**, p. 263.

[b] Braman, Journ. Biol. Chem., 1924, **60**, p. 79.

3.13 for experiments made between the twenty-fifth and the forty-eighth hours after food, and the factor 3.20 for experiments made more than 48 hours after food. Since the heat-production could not be directly determined in our apparatus, we were confronted with the alternative of computing the heat-production from the carbon-dioxide production either by means of the revised Armsby factor or by means of the calorific value of carbon dioxide at a known respiratory quotient. The heat-production of our fasting steers was accordingly computed for every experiment made by multiplying the measured carbon-dioxide production (*a*) by the above ratios and (*b*) by the calorific value of carbon dioxide at the respiratory quotient actually determined. A comparison of the heat values as computed on these two bases shows that in general when the respiratory quotient is not far from 0.82 the agreement in the two methods of calculation is close, but when, as is frequently the case in fasting experiments, the respiratory quotient is much nearer 0.70, the heat-production as computed by the factor obtained from Braman's data is almost invariably about 4 or 5 per cent lower than that computed from the calorific value of carbon dioxide at the known respiratory quotient. When the respiratory quotient is above 0.82, the reverse is true, the Braman factor giving higher results than the calculations from the respiratory quotient and the measured carbon-dioxide production. Since the Nutrition Laboratory has numerous calorimetric data available on other animals, which support the calculations of the heat-production from the carbon-dioxide production and the respiratory quotient, we feel more confidence in this latter method of computation. Hence this method has been employed in computing the heat-production in all instances where the respiratory quotient is 1.00 or below.

The calorific value of carbon dioxide has been well established for respiratory quotients between 0.70 and 1.00,[a] and varies from 3.408 calories per gram with a respiratory quotient of 0.70 to 2.569 calories per gram with a respiratory quotient of 1.00. There is still much discussion as to the calorific value of carbon dioxide and oxygen when the respiratory quotient is above 1.00, a situation which does not occur in fasting experiments, but not infrequently occurs in feeding experiments. A considerable amount of published experimental evidence[b] and, indeed, unpublished experiments of the Nutrition Laboratory with geese and with a pig which are also available, indicate that the calorific value of oxygen at a respiratory quotient above 1.00 is not essentially different from that at 1.00. Pending further and more elaborate direct determinations of the calorific value of oxygen at different respiratory quotients, therefore, the computation of the heat values reported in this monograph was carried out as follows in all cases where the respiratory quotient was over 1.00. The amount of oxygen actually involved in the metabolism is computed from the measured carbon-dioxide production (converted from grams to liters)

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[a] See Benedict and Talbot, Carnegie Inst. Wash. Pub. No. 201, 1914, p. 29, where values originally established by Zuntz have been retabulated.

[b] Rapport, Weiss, and Csonka, Journ. Biol. Chem., 1924, **60**, p. 583; Wierzuchowski and Ling, Journ. Biol. Chem., 1925, **64**, p. 697.

and the determined respiratory quotient, and the liters of oxygen thus found are multiplied by the factor 5.047, the calorific value of a liter of oxygen at a quotient of 1.00.

Under conditions where carbohydrate is converted into fat there is a splitting off of carbon dioxide unaccompanied by the absorption of oxygen, the so-called "atypical" carbon dioxide. In addition, there is the carbon dioxide produced by fermentations in the intestinal tract, and this production is not accompanied by any appreciable absorption of oxygen. Hence the whole situation, particularly with ruminants, is complicated by these two factors.

TABLE 38.—*Comparison of heat-production calculated by Andersen formula and from measured oxygen consumption*

Møllgaard experiment number	Heat produced per 24 hours		Difference	
	(*a*) Calculated by Andersen formula	(*b*) Calculated from oxygen consumption[1]	(*c*) Total ($b > < a$)	(*d*) Per cent $\left(\frac{c}{a} \times 100\right)$
	cal.	*cal.*	*cal.*	
10	8,431	8,496	+ 65	+0.77
11	10,505	10,419	− 86	−0.82
12	12,854	12,594	−260	−2.02
14	7,809	7,853	+ 44	+0.56
15	8,261	8,288	+ 27	+0.33
16	9,874	9,761	−113	−1.14
17	11,701	11,405	−296	−2.53
20	8,471	8,410	− 61	−0.72
21	10,098	10,201	+103	+1.02
22	10,210	10,069	−141	−1.38
23	11,690	11,704	+ 14	+0.12
24	12,413	12,179	−234	−1.89
25	12,691	12,569	−122	−0.96
26	13,143	12,777	−366	−2.78
27	13,350	13,227	−123	−0.92
30	9,197	9,260	+ 63	+0.69
31	9,946	10,044	+ 98	+0.99
32	10,802	10,753	− 49	−0.45
33	11,813	11,714	− 99	−0.84
34	12,235	12,114	−121	−0.99
35	13,922	13,702	−220	−1.58

[1] Assumed that each liter of oxygen is equivalent to 5.06 calories.

In this connection, a study of Møllgaard's[a] data obtained upon feeding ruminants is of interest. In computing the heat-production of his animals, Møllgaard makes use of the clever formula devised by his former associate, A. C. Andersen.[b] This formula, however, involves the determination of methane and the nitrogen in urine, as well as the gaseous determination of the carbon-dioxide production and the oxygen consumption. From unpublished experiments at the Nutrition Laboratory with surfeit feeding of

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[a] Møllgaard, Om Naeringsvaerdien af Roer og Byg til Fedning og om Naeringsstofforholdets Betydning for Fodermidlernes Naeringsvaerdi. Beretning 111, Forsøgslaboratoriet, Copenhagen, 1923.

[b] Andersen, Biochem. Zeitschr., 1922, 130, p. 143.

geese and pigs, however, we are convinced that the calorific value of oxygen remains remarkably constant, and when the total amount of oxygen actually absorbed by animals is known, and particularly when the respiratory quotient is at or near 1.00 (a condition always prevailing when ruminants are on maintenance rations), if the total oxygen consumption in liters is multiplied by the calorific value of oxygen for carbohydrates, namely, 5.06, the computed heat-production will be essentially that obtained by the Andersen formula. The advantage of this procedure is that it does not introduce into the heat computation the inherent errors of either the nitrogen determination or more particularly the complicated methane determination. In order to compare the heat values as computed by these two different methods we have summarized Møllgaard's experiments in Table 38. In the second column of this table are recorded his computations of the heat-production by the Andersen formula, the protein katabolized and the methane produced being taken into consideration. In the third column are recorded the heat values obtained by multiplying the oxygen determinations, as found with Møllgaard's respiration apparatus, by the calorific value of oxygen per liter, 5.06, when pure carbohydrates are being burned. It is seen from the last column in the table that in general the agreement between the two methods is within 1 per cent. Thus the simpler method of calculation lends itself to those experiments where nitrogen determinations are not available and methane can be determined only with difficulty, if at all. Indeed, this comparison raises the question as to whether for many experiments the actual determination of methane is of any significance in the computation of the energy output of the ruminant.

CONDITIONS PREREQUISITE FOR COMPARABLE MEASUREMENTS OF METABOLISM

With humans, certain conditions have been stipulated by common consent as being prerequisite for the measurement of the basal metabolism, if the results are to be on a comparable basis. Those factors known to influence basal metabolism most pronouncedly are thereby either entirely eliminated or in large part minimized by the prescribed conditions. Thus, the after-effect of food is minimized by insisting that the measurements be made at least 12 hours after the last meal, which should not be too large in amount or contain too large a proportion of protein. Some writers believe that a constant ration should be given for two or three days before the experiment, but this procedure is generally not carried out. The well-known influence of muscular activity is eliminated by insisting that the subject should be in complete muscular repose, and the after-effect of previous activity is ruled out by requiring that the subject should be lying down for at least a half hour before the measurements are made. Psychic disturbance must also be avoided, and the subject should be in a comfortable environmental temperature and with a normal body temperature.

In studying ruminants it is highly desirable to have some such equally satisfactory basis for securing comparable metabolism measurements. But practically all the conditions prescribed for the basal metabolism measurements of humans are impracticable with ruminants. The prolonged retention of food materials in the paunch of the ruminant makes the question of withholding of food a difficult one, and the point at which the true fasting-level is reached is not sharply defined. Some of our experiments throw light upon this subject (see p. 204). Enforced quiet is impracticable, since animals can not cooperate as can intelligent human beings. It is usually feasible to have the human subject rest quietly in bed, well covered, but animals will not lie down at command, nor will they remain motionless. In our earlier research on undernutrition in steers it became necessary to require certain easily insured conditions for the measurement of the "standard metabolism." It is a matter of regret that we chose this terminology, for Krogh,[a] with his critical insight, has objected to the term "basal metabolism" as determined with humans and wishes to propose the expression "standard metabolism." Our use of the expression was simply to designate that the metabolism was measured on a standardized basis for purposes of comparison. Admittedly, the metabolism, as so measured, could not have been the basal or lowest metabolism. The conditions prescribed for the measurement of the "standard metabolism" were that the animals should have been 24 hours without food, i. e., twice as long as in the case of humans, and that they should be standing.

A greater energy expenditure is seemingly required to support the animal body in the standing position than in the lying position. This difference due to the position of the body has long been a matter of experimental study, with widely differing results. Certain experiments which contributed information in a minor way on this subject were reported in our earlier monograph.[b] Under the special conditions of these tests it was found that the increment in metabolism due to standing was about 17 per cent. This difference between the metabolism in the standing and in the lying positions has of course no application to experiments made under standard conditions (which stipulate that the animal should be standing only), but it is of great significance in a long experiment of 24 hours, for example, when the animal at will alternates between standing and lying. In the latter case the attempt is made to compute the total metabolism for 24 hours on some basis of definite proportion between the time spent lying and standing. For all workers who employ the 24-hour period, some method of calculating the total 24-hour metabolism on a comparable basis is essential, since the animal will not either lie down or stand up for 24 hours. This matter will be discussed more at length in a later chapter (see pp. 211 to 213).

The most recent contribution on this point is the article published by Fries and Kriss,[c] who report some work carried out in Professor Armsby's laboratory. Although their final calculations are based exclusively on the data secured upon one cow, No. 874, weighing 400 kg., the experimental conditions were, they state, seemingly ideal. On the assumption that animals of varying weights would have a greater energy consumption when

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[a] Krogh, The respiratory exchange of animals and man, London and New York, 1916, pp. 56 et seq.

[b] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 215 et seq.

[c] Fries and Kriss, Am. Journ. Physiol., 1924, 71, p. 60.

standing than when lying in proportion to the two-thirds power of their body-weight, these authors propose a series of factors for correcting the total heat-production, as measured, to a standard day of 12 hours standing and 12 hours lying, for animals ranging in weight from 275 to 575 kg. Thus, they express the belief that with an animal of 275 kg. the "net energy per hour" is 20.5 calories greater when the animal is standing than when lying; with an animal of 400 kg. it is 26.3 calories greater, and with an animal of 575 kg. it is 33.5 calories greater. These factors are now regularly employed for application to all of the experimental work at the Pennsylvania Institute of Animal Nutrition.[a]

In view of the desirability of securing comparable metabolism measurements, all of the "standard metabolism" measurements reported in this present monograph were made 24 hours after food and with the steer in the standing position. During those fasting experiments and those experiments made immediately after the ingestion of feed, which involved short half-hour periods of measurement, the animals were likewise studied in most instances in the standing position, but the time intervals following food ingestion were of course greater or less than 24 hours. In the 3-day and 4-day experiments involving 8-hour periods of measurement, the steer was allowed to lie or stand at will. Since the 4-day experiments were made expressly to study the influence of the character and amount of food, the influence of fasting, and the influence of environmental temperature upon metabolism, it would seem as if a better comparison of the values obtained might be secured if the metabolism data were computed to a standard basis on the supposition that the animal would be standing 12 hours and lying 12 hours. The Pennsylvania investigators used this basis for their work because they found that usually their animals stood not far from 12 hours or half of the day. During the fasting experiments, however, our steers showed a disposition to lie down for a greater proportion of the time, and it is probable that a better basis for the comparison of the fasting data would be to compute the metabolism for perhaps 15 hours lying and 9 hours standing. Since the best method of handling such data is still problematical, however, the fasting metabolism of our steers has not been corrected to any uniform basis of lying and standing. (For further discussion of this point see p. 202.)

The Physiological Comparison of Animals

Comparison on the Basis of Live Body-weight

In comparing the metabolism of one animal with that of another, one of the simplest attempts to equalize differences in size has been to refer the metabolism to a uniform basis of body-weight. A large adult steer commonly weighs around 500 kg., and it has therefore been the custom to compute the heat-production of these large ruminants per 500 kg. of body-weight. Some writers have referred the heat-production to the two-thirds power of the body-weight. If physiologists are to accept the two-thirds power of the body-weight as an expression of the law of growth and the probable increase in active protoplasmic tissue, without reference to surface

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[a] Forbes, Science, 1926, 63, p. 311.

area, we are heartily in sympathy with this method of comparing the metabolism of animals of the same species but of different sizes. In all of our comparisons of the metabolism of our four fasting steers on the basis of live body-weight, however, we have computed the heat-production per 500 kg. of body-weight, which is practically the equivalent of the heat-production per kilogram of body-weight so commonly reported for man and small animals. We have not referred the metabolism to the two-thirds power of the body-weight, since this computation brings in the surface-area factor and we have felt that it is better to compute the surface area in a different way.

Comparison on the Basis of Body-surface

The persistent popularity of the conception that the surface area is an important factor controlling metabolism and the persistent efforts of physiologists to compare the metabolism of individuals of different ages and sizes and under different conditions of nutrition on the basis of the heat-production per unit of surface area make it necessary to compare the metabolism of animals on this same basis, irrespective of any personal credence in the significance of this comparison. For many years the general conception has prevailed that the metabolism of warm-blooded animals is proportional to the surface area of the animal and that the basal heat-production per square meter of body-surface per 24 hours is essentially the same (i. e., not far from 1,000 calories) with all warm-blooded animals, regardless of species, size, or age. It was recognized by Rubner, however, that the heat-production of different individuals per square meter of body-surface is the same only under the same general conditions of nutrition. Yet the extensive use of the surface area as a basis for the comparison of metabolism in pathological cases necessarily includes a large proportion of humans in a poor state of nutrition. Since such comparisons have been made without the slightest reservations on the part of medical men, it therefore seems proper to compute the heat-production per square meter of body-surface of our steers, although we fully recognize that they were not in the same nutritive condition at all times and hence should not, strictly speaking, be compared on this basis. Indeed, the Nutrition Laboratory is distinctly out of sympathy with the general belief that the metabolism of all warm-blooded animals is the same per unit of surface area. The method of comparison is, however, justified on the basis of usage, provided a false significance is not attached to it and that a causal relationship between body-surface and heat-production is not insisted upon.

METHOD OF ESTIMATING THE SURFACE AREA OF FASTING STEERS

It is unnecessary at this point to discuss the basis and derivation of the so-called "surface-area law," for this subject has been considered extensively in an earlier publication of the Nutrition Laboratory.[a] If comparisons of the metabolism are to be made, however, with reference to the surface area, the measurement of this factor must be accurate. In the

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[a] Harris and Benedict, Carnegie Inst. Wash. Pub. No. 279, 1919, pp. 129 et seq.

literature, new formulas for estimating body-surface, employing constants of various sizes, are continually appearing. The experimental bases for these constants will not, we believe, withstand the closest criticism. Thus, Du Bois[a] has shown clearly the great error possible in the constant in Meeh's[b] formula, so generally used for computing the body-surface of humans. Actual measurements of the surface area of other animals are scarce, and the computation of the surface area of animals of various sizes still remains debatable. Du Bois[c] has placed the body-surface measurements of humans upon an accurate footing, and for this reason probably more is known about the surface area of humans than of any other living organism at the present time, but knowledge with regard to the surface area of ruminants is by no means so definite or complete.

In the attempt to approximate as closely as possible the probable surface area of our first groups of steers which were subjected to undernutrition, the earlier literature regarding body-surface measurements, and particularly the more recent extensive measurements of Moulton,[d] were considered. In Moulton's formula the warm, empty weight of the animal after slaughter enters into the calculation. It was impossible in our work with steers to determine the warm, empty weight and it therefore had to be computed. In the estimation of the surface areas of our animals studied in the research on undernutrition their relative nutritive states, as appraised by an expert judge of livestock, were used as bases for assumptions of the probable warm, empty weights and Moulton's formula ($S = W^{5/8} \times 0.1186$) involving the use of the warm, empty weight was employed. This method of computation was given extensive treatment in our earlier monograph.[e] Since this monograph was published, an article by Hogan and Skouby[f] (who succeeded Moulton) has appeared, in which changes are suggested in Moulton's body-surface formula, the chief of which is the elimination of the difficult determination of the warm, empty weight by the use of a different constant. Thus, the five-eighths power of the live weight of the animal is multiplied by the constant 0.1081 instead of 0.1186, and Hogan finds that the surface areas as thus computed are confirmed by areas computed by a second formula in which the length of the animal is taken into consideration.

Although the use of the warm, empty weight undoubtedly is of value in many connections and is proposed urgently by Moulton for live animals, the uncertainty regarding the amount of the fill makes it difficult to approximate such a weight. Particularly is this true during the pronounced transitory stage of the contents of the intestinal tract incidental to prolonged fasting. The actual number of cases where an animal has been slaughtered after fasting and the fill determined are so few that almost nothing is known with regard to the amount of fill in cattle under such conditions. The early observations of Grouven indicate that the mass of

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[a] Du Bois and Du Bois, Arch. Intern. Med., 1915, **15**, p. 868.

[b] Meeh, Zeitschr. f. Biol., 1879, **15**, p. 425.

[c] Du Bois and Du Bois, Arch. Intern. Med., 1916, **17**, p. 863.

[d] Moulton, Journ. Biol. Chem., 1916, **24**, pp. 303 et seq.; Armsby, Fries, and Braman, Journ. Agric. Res., 1918, **13**, p. 47; Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta. Bull. 18, 1915, pp. 11 and 41.

[e] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 220 et seq.

[f] Hogan and Skouby, Journ. Agric. Research, 1923, **25**, p. 419.

fill was not materially decreased in his fasting oxen, although the amount of dry matter decreased enormously.

In attempting to approximate the surface areas of our fasting steers, we at first employed the same formula as with the steers on undernutrition, i. e., Moulton's formula involving the use of the warm, empty weight. Estimates of the various nutritive states and the probable fill had to be made in order to use this formula, and aberrant results were invariably found which could not be explained. In a few cases the lengths of our animals were known, although these lengths were not exactly the same as that used by Hogan in his body-surface formula. Nevertheless, it was believed that these lengths, although subject to a slight correction, could properly be used, and accordingly for one of our animals the body-surface was calculated during and preceding a fasting period, upon the basis of Hogan's formula, i. e., $S = W^{0.4} \times L^{0.6} \times 217.02$. In this formula W represents the live weight of the animal in kilograms, L the length of the body in centimeters from the point of withers to the end of the ischium, and 217.02 is the constant for cattle. With this formula, Hogan maintains that the body-surface can be computed with a maximum error of less than ± 5.5 per cent. A comparison of the body-surface of one of our fasting steers as computed from Moulton's formula involving empty weight, from Hogan's length formula, and from Hogan's modification of the Moulton formula ($S = W^{5/8} \times 0.1081$), indicates that fairly closely agreeing results can be obtained by the two latter methods and that less aberrant values are thus obtained for the body-surface of steers during periods of fasting and realimentation. Hence, since the lengths of our fasting animals were determined only once throughout the entire experimental series, we have felt justified in using in all of the body-surface computations reported in this monograph the formula $S = W^{5/8} \times 0.1081$, in which W is the live

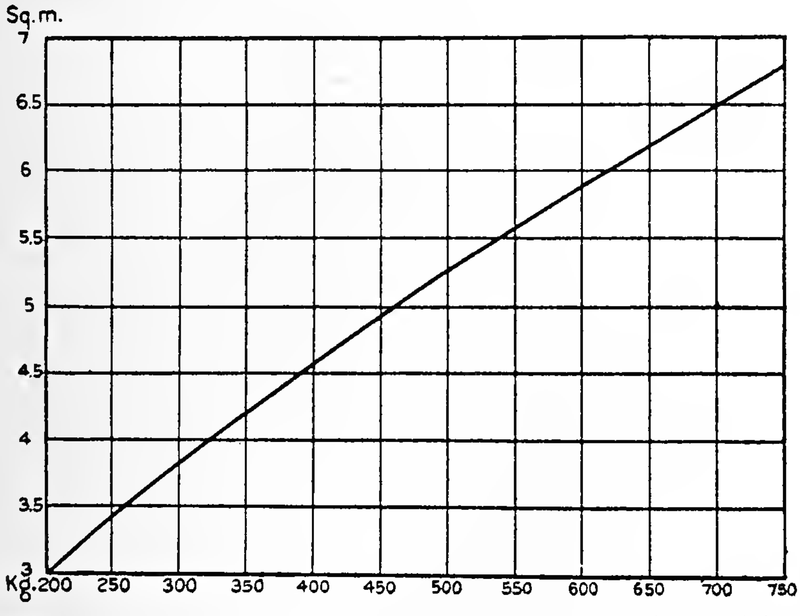

FIG. 8.—Body-surface in square meters referred to live weight in kilograms.

The body-surface is computed from the formula $S = W^{5/8} \times 0.1081$, in which W represents the live weight.

weight. Indeed, so satisfactory have we found this formula and so convinced are we that this is the best available approximation of the true surface area, that we have plotted a curve giving the surface areas of animals with live weights ranging from 200 to 750 kg. (See Fig. 8.) This curve, as the nature of the formula will show, is not a straight line, but from it the surface area can be read directly, if the live weight of the animal is known. In considering the heat-production per square meter of body-surface in this monograph, all of the areas employed in our calculations were taken from this curve.

In thus emphasizing the desirability of securing the greatest accuracy in computations of the surface area of these animals, we wish to affirm that whatever the value of the actually known surface area of these animals may be, we can not subscribe to the prevailing notion that the surface area is indissolubly associated with the heat-production, and in this report the heat-production has been calculated per unit of surface area solely as a concession to the large number of physiologists who are still wont to think of the heat-production from this singular point of view.

Method of Presenting the Gaseous Metabolism Data

The large mass of data accumulated in this research may best be considered, not in the chronological order of the experiments, but by grouping the data according to the various problems studied. Separate treatment will therefore be given to the metabolism measurements under three main heads, i. e., the fasting experiments, the standard metabolism experiments, and the experiments in which the effect of the ingestion of food was studied.

The fasting experiments themselves will be discussed in three general groups. The fasts of 5 to 14 days and the short 2-day and 3-day fasts represent one group made with the same general technique, although at different nutritive levels. Thus, in these experiments the metabolism was usually measured during 4 half-hour periods with the animal in the standing position. This type of experiment comprises the bulk of the metabolism measurements. In these experiments the metabolism was measured only for a period of about 1½ or 2 hours, and although the results have been computed to the 24-hour basis, the values must of necessity be somewhat higher than they would have been had the metabolism been measured during the total 24 hours, for the conditions of the experiment required that the animal should always be standing. A second group of fasting experiments was therefore made, to secure a complete picture of the 24-hour metabolism. In these experiments the metabolism was measured in consecutive 8-hour periods during 3 continuous days, beginning 24 hours after withdrawal of food, and the animal was allowed to lie or stand at will. Finally, to throw light upon the transitional period between feeding and fasting, with particular reference to the character and amount of the previous feed-level, and also to throw light upon the influence of environmental temperature, a third group of experiments was made. In this series the metabolism was measured in consecutive 8-hour periods and each experiment lasted for 4 days, comprising 2 days on feed followed by 2 days of fasting.

Table 39.—*Respiratory quotients of steers during fasts of 5 to 14 days*

Steer and dates of fasts	On feed before fast		Days fasting												
	Hours after feed	R. Q.	1	2	3	4	5	6	7	8	9	10*	12	13	14
			Hours without food												
			22 to 32	42 to 56	65 to 80	89 to 104	113 to 128	137 to 149	168 to 174	192 to 200	216 to 228	241 to 245	291 to 300	312 to 315	336 to 339
Steer C:															
Apr. 17 to May 1, 1922	5	1.18	0.89	0.82	[1](0.73)	0.73	0.73	[2][0.70]	......	......	......	......	0.70	[1](0.70)	[1](0.70)
June 1 7, 1922....	4 to 6	.96	.85	.75	.73	.70	......	[2][.70]	......	......	......	......	......	......	......
Nov. 6 16, 1922....	2 4	1.01	.74	.76	.73	[1](.72)	.72	......	......	[2][0.70]	[2][0.70]	......	......	......	......
Nov. 4 10, 1923....	18 19	.93	......	.79	.74	.73	.72	.70	......	......	......	......	......	......	......
Mar. 3 13, 1924....	......	......	.82	.74	.71	.70	.70	.71	0.70	.70	.71	0.70	......	......	......
Steer D:															
Apr. 17 to May 1, 1922	8	.99	.97	.83	.75	.75	.74	.73	......	......	......	......	[1](.70)	[1](.70)	[1](.70)
June 1 6, 1922....	1 to 3	1.17	.77	.73	.70	.71	[2][.70]	......	......	......	......	......	......	......	......
Nov. 6 14, 1922....	7 8	.86	......	.72	.71	[1](.71)	......	[1](.70)	[1](.70)	......	......	......	......	......	......
Nov. 4 9, 1923....	......	......	.86	.76	.72	.72	.71	......	......	......	......	......	......	......	......
Mar. 3 12, 1924....	......	......	.73	.73	.70	.70	[1](.70)	[1](.70)	.70	.70	.71	......	......	......	......
Steer E:															
Feb. 12 to 17, 1924....	......	......	.84	.72	[2][.70]	[2][.70]	......	......	......	......	......	......	......	......	......
Steer F:															
Feb. 12 to 18, 1924....	......	......	.78	.73	[2][.70]	......	.72	......	......	......	......	......	......	......	......

[1] Assumed, since quotients actually determined seemed aberrant.

[2] Based on quotients slightly below 0.70.

* No determinations of the respiratory quotient were made on the eleventh day.

In presenting these data it is deemed best to record in the various tables not only the actual measurements of the carbon-dioxide production and the respiratory quotient, but the derived computations of the heat-production and other related measurements obtained during the same 24 hours as the gaseous metabolism measurement, i. e., the records of the heart-rate, the insensible loss, and the environmental temperature.

METABOLISM DURING FASTING

RESPIRATORY QUOTIENT

The determination of the respiratory quotient is of value in two respects. In the first place, the respiratory quotient indicates the character of the metabolic processes during the period of experiment. When the steer is receiving full feed, the respiratory quotient will be above 1.00, indicating carbohydrate combustion. When feed is withdrawn, the quotient will fall as the fast progresses and ultimately will reach a value not far from 0.70, characteristic of fat combustion. Inasmuch as practically all of our experiments dealt with the early and late stages of fasting, the determinations of the respiratory quotient therefore serve to indicate the rapidity at which the metabolism reaches the fasting-level. The second, and perhaps the most important, use of the respiratory quotient is that it indicates the calorific value of carbon dioxide to be used in the calculation of the heat-production. Since the carbon-dioxide production of the steers was actually determined, as well as the relationship between the carbon-dioxide production and the oxygen consumption, i. e., the respiratory quotient, it is possible to compute, on the one hand, the oxygen consumption, and, on the other hand, to secure a more accurate factor for the calorific value of carbon dioxide in the computation of the probable heat produced.

The respiratory quotient plays its greatest rôle in our researches as an index of the probable calorific value of carbon dioxide. Consequently, before the discussion of the quantitative amount of carbon dioxide produced, and particularly of the heat relationships, a consideration of the actually determined respiratory quotients is desirable. The determinations made during the series of fasts of 5 to 14 days will first be examined, and the data are accordingly given in Table 39. The results have been computed only to two significant figures.

The first fast for which respiratory quotients could be determined was the longest one of 14 days, because the Carpenter gas-analysis apparatus was not installed in time to make analyses for the first two fasts. It is perhaps not surprising, therefore, that seemingly aberrant quotients were occasionally found. It has been assumed that quotients less than 0.70 in all probability represent technical errors. Accordingly, in those instances where the gas analyses gave quotients slightly below 0.70, a quotient of 0.70 has been assumed, since this value is not far from the quotient actually found. Irrespective of this fact, the general picture of the trend of the respiratory quotient as the fast progresses is clear. Prior to the different fasts the quotient was about 1.00 or above, depending somewhat upon the character of the food and probably the time since the last food was taken. On the first day of fasting, i. e., 22 to 32 hours after food, when there was still considerable material in the intestinal tract, the quotient is considerably below 1.00 in most instances, ranging from 0.73 to 0.97, and being on the average 0.83. On the second day of fasting there is a further drop with all four steers. On the third day the quotients of steer D are slightly lower. The values for steer C tend to be a little higher than those for steer D on the third day, although one must speak of a variability of 0.02 in the respiratory quotient with considerable reserve. After the third day the quotients are essentially constant. The small amounts of food given to the steers following the fasts almost invariably resulted in an increase in the quotient, this increase depending upon the time when digestion began and the amount of carbohydrate actually burned.

In the fasts of December 1921 and January 1922, with steers C and D, the respiratory quotient was not determined, and it was necessary in the computation of the heat values for these fasts to assume quotients, which, as a matter of fact, are based upon average values derived from Table 39. Additional information regarding the respiratory quotients during the first few days of fasting was secured in the series of short 2-day and 3-day fasts, and this evidence was also used in making the assumptions of the most probable quotients to be used for the first two long fasts. These data are given in Table 40, from which it is seen that 25 to 26 hours after food ingestion the respiratory quotient is 0.83 on the average, and that 47 to 50 hours after food it is 0.76. In January 1923, a 3-day fast was carried out with each animal, and a quotient of 0.72 was noted with steer C and 0.70 with steer D, 72 hours after food.

TABLE 40.—*Respiratory quotients of steers 24 and 48 hours after food (maintenance level of nutrition)*

Steer and dates of fasts (1923)	Hours without food		Steer and dates of fasts (1923)	Hours without food	
	25 to 26	47 to 50		25 to 26	47 to 50
Steer C:			Steer D:		
Jan. 4 and 5....	0.83	[1]0.73	Jan. 10 and 11....	0.83	[1]0.73
Jan. 22 and 23....	.83	.76	Jan. 18 and 19 ...	.81	.74
Jan. 29 and 30....	.82	.73	Jan. 26 and 27....	.82	.78
Feb. 6 and 7....	.83	.73	Feb. 2 and 3....	.86	.75
Feb. 12 and 13....	.84	.74	Feb. 9 and 10....	.78	.77
Feb. 19 and 20....	.82	.70	Feb. 15 and 16....	.82	.75
Mar. 2 and 3....	.83	.79	Feb. 23 and 24....	.83	.73
Mar. 9 and 10....	.84	.77	Mar. 6 and 7....	.83	[2] (.75)
Mar. 16 and 17....	.80	.77	Mar. 14 and 15....	.84	.79
Mar. 23 and 24....	.86	.79	Mar. 21 and 22....	.86	.76
Average.....	.83	.75	Average....	.83	.76

[1] Determinations made 72 hours after food in the January experiments showed a quotient of 0.72 for steer C and 0.70 for steer D.

[2] Assumed; not included in average.

In view of the picture shown by the respiratory quotients in Tables 39 and 40, and in consideration of the fact that the true fasting state is represented by a katabolism essentially of fat, it can be seen that the steer is burning essentially fat on the third day of fasting. The effect of the previous state of nutrition is not so pronounced as was at first thought would be the case. Thus, as seen from Table 39, the respiratory quotient noted with steer C in the fast in March 1924, following submaintenance feeding, was 0.82 on the first day and 0.74 on the second day. An even lower quotient of 0.74 on the first day was found in the fast following pasture in November 1922. On the other hand, the lowest respiratory quotient on the first day of fasting, namely, 0.73, was noted with steer D in the fast following submaintenance feeding in March 1924. The general picture, however, is that a fat combustion occurs not far from the third day of fasting.

Further data regarding the influence of different feed-levels upon the respiratory quotient during the first day of fasting were secured in the series of "standard metabolism" experiments, in which the animals were studied 24 hours after their last feed, both at a maintenance and a submaintenance level of nutrition. In 28 experiments during maintenance feeding the average respiratory quotient of steer C was found to be 0.84, and in 27 experiments with steer D it was found to be 0.83. Following submaintenance feeding, steer C had an average respiratory quotient for 12 experiments of 0.80, and steer D had an average quotient for 14 experiments of 0.77. (See Tables 55 and 56, pp. 226 and 227, for details.)

TABLE 41.—*Respiratory quotients as affected by ingestion of food, steers C and D*

Steer and date	Last feed before experiment		Hours without food	Respiratory quotient (average)	Daily feed-level for at least 2 weeks prior to experiment
	Hay	Meal			
Steer C:	*kg.*	*kg.*			
May 31, 1922	3.2	2.0	0 to 4	1.12	9 kg. hay; 4 kg. meal.
June 1, 1922	4.5	2.0	4 6	0.96	Do.
Nov. 6, 1922	Grass		2 4	1.00	Pasture.
Mar. 28, 1923	3.6	1.0	2 4	1.06	9 kg. hay; 2 kg. meal.[1]
Apr. 9, 1923	3.8	......	2 4	0.96	Do.
Apr. 16, 1923	4.5	......	2 3	1.07	Do.
Nov. 5, 1923	Grass		18 20	0.93	Pasture.
Steer D:					
Apr. 5, 1922	4.5	1.5	8 10	1.10	9 kg. hay; 3 kg. meal.
Apr. 17, 1922	4.5	1.5	8 9	0.99	Do.
May 31, 1922	3.9	2.0	7 9	0.88	9 kg. hay; 4 kg. meal.
June 1, 1922	2.7	2.0	¾ 3	1.17	Do.
Nov. 6, 1922	Grass		7 8	0.86	Pasture.
Mar. 27, 1923	3.6	1.0	3 4	1.08	9 kg. hay; 2 kg. meal.[1]
Apr. 10, 1923	4.5	......	2 3	1.16	Do.
Apr. 17, 1923	4.5	......	2 4	1.03	Do.

[1] Intermittent 2-day fasts between Jan. 4 and Mar. 24.

In this consideration of respiratory quotients no special attention has been paid to the presence of methane and no attempt has been made to differentiate between the carbon dioxide of fermentation and cleavage and the carbon dioxide of true metabolism. The respiratory quotients reported represent the actual determinations with the Carpenter gas-analysis apparatus. In general, the data show that the ruminant is somewhat sluggish in adjusting himself to a fat combustion during fasting (which is to be expected, owing to the large amount of feed residues in the intestinal tract), but almost immediately responds to the ingestion of carbohydrate following a fast of several days.

The influence of the ingestion of food upon the respiratory quotient under normal conditions of feeding and normal body reserves is well brought out in Table 41. Several short experiments, comprising usually 4 half-hour periods, were made during the first few hours after food ingestion. The feed varied from pasturage to a maximum of 4.5 kg. of timothy hay and 2 kg. of meal. In these experiments the respiratory quotient as a rule was found to be about 1.00 or, in some cases, a little higher. The average respiratory quotient of both animals in the 15 experiments reported in Table 41 is 1.02.

Carbon-dioxide Production

Carbon dioxide, as the main gaseous product studied in connection with these researches (the respiration chamber being designed in the first place for the determination of this compound), assumes the greatest significance in the study of the metabolism of these steers. It was recognized at the start that the various sources of carbon dioxide are complex with the ruminant. There is, first, the carbon dioxide resulting from the true oxidation of body material, be it glycogen, body protein, or body fat. There is, in addition, a transformation of soluble carbohydrate to fat, with the cleavage of carbon dioxide, the so-called "atypical" carbon dioxide, and, finally, there is an appreciable production of carbon dioxide as a result of the process of fermentation. Because of the reduction in digestive processes and in energy transformations which occur during fasting, however, the measurement of carbon dioxide alone is of great value. In our research on the undernutrition of steers it was found that when the animals were on a maintenance feed-level, i. e., not burning fat, and when they were on a submaintenance feed-level, i. e., scantily fed and drawing upon body material, the carbon-dioxide production was extremely suggestive of the energy transformations. With the elimination of feeding and the rapid drafts upon body stores and available material in the intestinal contents, the carbon-dioxide production becomes an even clearer index of the true metabolic process than is the case during any condition of feeding. This state is reached rapidly after the first day of fasting, when the metabolism may be complicated by the combustion of material amounts of carbohydrate substances.

Accurate measurements of the carbon-dioxide production were therefore obtained throughout the entire series of respiration experiments. Except during the last year, the periods of measurement, as already stated, were usually 30 minutes in length, and the values reported for the carbon-dioxide production are based in general upon four consecutive, well-agreeing periods, the animal being with few exceptions always in the standing position. During the last year of the experimental series the periods were 8 hours in length. The discussion in this chapter, however, will be confined to the average values based on the half-hour periods with the animal standing.

Theoretically, the respiratory quotient should not be affected by the size or weight of the animal, but the amount of carbon dioxide produced is directly proportional, in general, to the size of the animal. In the presentation of the data, however, it seems best to consider, first, the actual measurements of carbon dioxide expressed in grams per half hour, on the assumption that, although in any particular fast the animal starts at a definite weight and loses weight as the fast goes on, the changes in body-weight are not great, and the measurements of the carbon-dioxide production are, therefore, more or less comparable. On this basis, steers C and D may be compared with each other and steers E and F with each other, but since the two latter steers are smaller and younger animals, they may not be directly compared with the older animals, C and D, without further consideration of their body-weights.

The carbon-dioxide measurements made in connection with the fasts of 5 to 14 days are recorded in Table 42. An examination of the data for steers C and D shows that prior to the fast the carbon-dioxide production varies from 120.5 to 172.2 grams per half hour, depending largely upon the nature and amount of the feed received. On the first day of fasting, the decrease in the carbon-dioxide excretion is enormous, amounting to almost 50 per cent in two of the cases where it is possible to make the comparison with measurements secured prior to fasting. Average values for steers C and D for the carbon-dioxide production on the first day of fasting can hardly be derived from the data in this table, since the March fast followed submaintenance feeding and the two November fasts followed pasture feeding. On the second day of fasting there is a still further decrease in the carbon dioxide produced, amounting to not far from 20 grams in the first four fasts of steers C and D which followed maintenance feeding, and amounting to 12 and 8 gm., respectively, with steers C and D in the fast at a submaintenance level. On the third day there is in general a still further decrease, save in the March fast of steer C following submaintenance rations. On the fourth day the decrease is somewhat less, amounting usually to but 3 or 4 gm. On the fifth day nearly a constant value is reached, and for several days thereafter no great change in the elimination takes place. In the 14-day fasts, however, there is a still further fall. Thus, in the case of steer C, a minimum value of 43.6 gm. is reached on the fourteenth day, and in the case of steer D a minimum value of 47.4 gm. is found on both the tenth and the fourteenth days.

Throughout the fast following submaintenance rations in March 1924, the carbon-dioxide elimination is on a distinctly lower plane, a minimum of 40.7 gm. being found with steer C on the last day and a minimum of 44.3 gm. with steer D on the eighth day. With the two younger animals, steers E and F, which fasted following submaintenance feeding, there is essentially a continuous decrease as long as the fasts lasted, i. e., for 4 or 5 days.

In certain experiments food was given immediately after the fast, and in all of these instances the carbon-dioxide excretion increased appreciably, although the time after feeding was relatively short and the amount of food actually eaten was small, as these animals were very deliberate in their first feeding after a prolonged fast.

TABLE 42.—*Carbon-dioxide elimination before and during fasts of 5 to 14 days*

(Average values in grams per half hour)

Steer and dates of fasts	On feed before fast		Days fasting													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14
			Hours without food													
	Hours after feed	CO₂	22 to 32	42 to 56	65 to 80	89 to 104	113 to 128	137 to 149	168 to 174	192 to 200	216 to 228	241 to 245	267 to 272	291 to 300	312 to 315	336 to 339
Steer C:																
Dec. 6 to 13, 1921	......	......	76.1	62.1	55.1	52.8	51.4	50.3	49.6	......	......	......	......	......	......	......
Jan. 4 14, 1922	......	......	79.4	70.8	60.9	52.6	55.0	51.6	51.4	47.3	51.0	52.9	......	......	......	......
Apr. 17 May 1, 1922	5	147.6	79.6	59.5	56.0	52.4	51.6	51.8	48.0	51.1	51.1	47.6	45.9	46.9	44.9	43.6
June 1 7, 1922	4 to 5	133.5	80.6	63.8	52.6	52.4	......	53.9	......	......	......	......	......	......	......	......
Nov. 6 16, 1922	2 to 3	120.5	[1] 84.3	[1] 72.6	[1] 66.4	[1] 58.1	[1] 59.8	......	......	58.5	61.9	......	......	......	......	......
Nov. 4 10, 1923	18 to 19	125.3	......	81.7	67.7	59.3	62.5	63.5	......	......	......	......	......	......	......	......
Mar. 3 13, 1924	......	......	55.1	42.8	43.8	44.4	44.5	44.2	45.8	44.9	44.7	40.7	......	......	......	......
Steer D:																
Dec. 6 to 13, 1921	......	......	85.6	63.8	61.3	58.1	56.1	54.1	53.0	......	......	......	......	......	......	......
Jan. 4 14, 1922	......	......	84.9	67.3	60.3	56.3	56.3	52.4	53.9	49.6	50.6	51.3	......	......	......	......
Apr. 17 May 1, 1922	8	137.3	83.4	67.8	59.5	54.4	53.0	51.9	50.8	51.0	49.8	47.4	51.0	48.0	47.5	47.4
June 1 6, 1922	1 to 3	172.2	83.7	67.7	64.1	57.5	61.2	......	......	......	......	......	......	......	......	......
Nov. 6 14, 1922	7 to 8	126.9	......	80.7	71.3	69.8	......	63.1	60.0	......	......	......	......	......	......	......
Nov. 4 9, 1923	......	......	117.4	86.2	71.4	70.4	62.9	......	......	......	......	......	......	......	......	......
Mar. 3 12, 1924	......	......	67.9	59.3	53.8	53.0	49.5	55.7	51.4	44.3	45.0	......	......	......	......	......
Steer E:																
Feb. 12 to 17, 1924	......	......	38.0	35.0	30.9	31.7	......	......	......	......	......	......	......	......	......	......
Steer F:																
Feb. 12 to 18, 1924	......	......	37.5	36.4	36.1	......	33.9	......	......	......	......	......	......	......	......	......

[1] Measurement made during period of lying and standing

In general, during these long fasts, the carbon-dioxide production falls off rapidly during the first three or four days. The decrease usually continues until the end of the fast and is followed by a rapid rebound after the ingestion of even small amounts of relatively indigestible hay or meal mixtures. In the fasts at a submaintenance level, particularly with steers C and D, the total amounts of carbon dioxide involved, even on the first day of fasting, are lower than in any of the other fasts. Indeed, on the second day in the March fast of steer C a value of 42.8 gm. per half hour was noted, which is lower than any other value found with this animal, even at the end of the 14-day fast. On the other hand, the submaintenance ration did not affect so profoundly the carbon-dioxide elimination of steer D, for it is not until the eighth day of his fast following submaintenance rations that a minimum value of 44.3 gm. is found, which is lower than that found in any of the fasts following maintenance feeding. This difference in the metabolism of two otherwise presumably comparable animals will be noted frequently throughout the rest of this discussion of the gaseous metabolism (see, especially, p. 180).

In a series of 2-day and 3-day fasts with steers C and D at a maintenance level of nutrition, carbon-dioxide measurements were also secured. These are recorded in Table 43. In the case of steer C, it is seen that when he had been 25 to 26 hours without food his carbon-dioxide production per half hour was, on the average for the 10 measurements made, 71.0 gm. This value is somewhat lower than the values shown in Table 42 for steer C on the first day of the fasts at a maintenance level, and it is more nearly in line with the average value to be found for this animal in Table 42 on the second day of fasting. With steer D, the average value for the 10 experiments reported in Table 43 is 79.5 gm., materially less than the values recorded in his case for the first day of fasting in Table 42.

TABLE 43.—*Carbon-dioxide production of steers per half hour, 24 and 48 hours after food*
(Maintenance level of nutrition)

Steer and dates of fasts (1923)	Hours without food		Steer and dates of fasts (1923)	Hours without food	
	25 to 26	47 to 50		25 to 26	47 to 50
Steer C:	*gm.*	*gm.*	Steer D:	*gm.*	*gm.*
Jan. 4 and 5....	66.6	[1]59.2	Jan. 10 and 11....	79.6	[1]64.8
Jan. 22 and 23....	56.8	62.8	Jan. 18 and 19....	76.5	53.1
Jan. 29 and 30....	77.8	43.1	Jan. 26 and 27....	82.6	50.8
Feb. 6 and 7....	67.2	65.9	Feb. 2 and 3....	74.0	59.6
Feb. 12 and 13....	69.8	61.7	Feb. 9 and 10....	75.6	67.3
Feb. 19 and 20....	74.6	73.0	Feb. 15 and 16....	83.6	85.6
Mar. 2 and 3....	73.2	59.3	Feb. 23 and 24....	79.8	73.7
Mar. 9 and 10....	71.8	69.0	Mar. 6 and 7....	80.2	75.1
Mar. 16 and 17....	71.9	58.7	Mar. 14 and 15....	79.7	72.3
Mar. 23 and 24....	80.5	65.2	Mar. 21 and 22....	83.7	68.0
Average.....	71.0	61.8	Average....	79.5	67.0

[1] Determinations made 72 hours after food in the January experiments showed a carbon-dioxide production of 55.3 gm. with steer C and 54.5 gm. with steer D.

On the second day of the short fasts, when the steers had been 47 to 50 hours without food, the average carbon-dioxide production was 61.8 and 67.0 gm. per half hour with steers C and D, respectively, values more nearly like those noted on the second day of the longer fasts.

The differences noted between the series of short fasts and the series of longer fasts in the carbon-dioxide production on the first day of fasting, and the general differences between the two series of fasts, are excellent demonstrations of the fact that the carbon-dioxide production on the first day of fasting is so irregular as to make its use as an index of heat-production of doubtful value without careful consideration of the respiratory quotient. The respiratory quotient also varies on the first day, as can be seen from Table 39, page 157. The differences noted in the two series may in part be explained by differences in prior feed conditions, the effect of repeated short fasts, and indeed, differences in environmental temperature.

Tabular Presentation of Data for Long and Short Fasts

The data accumulated in this fasting research were so extensive that space will not permit of publishing all the details, and it is possible to present only condensed abstracts. During the experimental season from December 1921 through March 1924, steers C and D fasted at intermittent intervals for periods of from 2 to 14 days, or a total of 80 and 76 days, respectively. The pertinent data for these fasts have been summarized in Tables 44 and 45. Similar data for the fasts of steers E and F in February 1924 have been summarized in Table 46. The gaseous-metabolism measurements reported for all these fasting days were obtained 22 hours or more after the last food was given, and in every case represent average values for three or four well-agreeing periods, each of 30 minutes' duration. In all instances the animal was in the standing position, unless otherwise indicated in the tables. The accuracy of the respiration chamber was frequently controlled throughout this time by introducing and recovering known amounts of carbon dioxide. (See p. 36.)

The live weight reported for the first day of fasting, i. e., when the animal had been for 24 hours without food, represents an average weight based upon the weight on the given date and the weights for 6 days preceding or for as many days preceding up to six for which live weights were available. For each fasting day after the first the weights represent individual weights obtained at 2 p. m. of the given date, in all cases except the fasts in March 1924, with steers C and D, when the weights were recorded at 7 a. m. because the 24-hour periods began and ended at that time. The heart-rates recorded in these tables represent those records secured nearest to the time of the respiration experiment, either shortly before or shortly after the experiment. The values for the insensible perspiration and for the stall temperature are for the 24-hour periods from 2 p. m. of the preceding date to 2 p. m. of the given date in all fasts except those of steers C and D in March 1924, when the 24-hour periods began at 7 a. m. The respiration experiments were usually made during the morning of the given date, so that the values for insensible perspiration and similarly for the stall temperature represent essentially the 24-hour period preceding the

TABLE 44.—*Metabolism of steer C when fasting at different levels of nutrition*

Date	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Hours without food to beginning of experiment	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours		
									Total	Per 500 kg.	Per sq. m.
1921	*kg.*		*kg.*	°*C.*		°*C.*	*gm.*		*cal.*	*cal.*	*cal.*
Dec. 7....	584.8	44	4.0	5	28	....	76.1	(0.82)	10,900	9,300	1,880
Dec. 8....	561.4	34	3.4	5	52	17.0	62.1	(.76)	9,500	8,500	1,680
Dec. 9....	550.0	32	1.6	15	76	20.6	55.1	(.73)	8,700	7,900	1,560
Dec. 10....	543.4	36	3.2	20	97	19.3	52.8	(.72)	8,400	7,700	1,520
Dec. 11....	543.4	....	2.8	18	121	19.3	51.4	(.71)	8,300	7,600	1,500
Dec. 12....	538.2	....	2.2	17	146	18.8	50.3	(.70)	8,200	7,600	1,490
Dec. 13....	533.2	....	2.2	20	169	23.0	49.6	(.70)	8,100	7,600	1,480
1922											
Jan. 5....	588.2	48	11.6	20	27	24.3	79.4	(.82)	11,400	9,700	1,960
Jan. 6....	570.6	38	7.0	20	51	21.9	70.8	(.76)	10,800	9,500	1,890
Jan. 7....	564.4	38	4.8	20	75	20.0	60.9	(.73)	9,600	8,500	1,690
Jan. 8....	555.6	36	5.4	21	97	21.5	52.6	(.72)	8,400	7,600	1,500
Jan. 9....	549.0	38	3.6	24	123	24.8	55.0	(.71)	8,900	8,100	1,600
Jan. 10....	548.2	38	4.2	20	147	21.3	51.6	(.70)	8,400	7,700	1,510
Jan. 11....	539.6	36	4.0	20	171	18.7	51.4	(.70)	8,400	7,800	1,520
Jan. 12....	536.2	30	3.6	21	196	20.8	47.3	(.70)	7,700	7,200	1,400
Jan. 13....	538.4	34	3.6	23	219	22.9	51.0	(.70)	8,300	7,700	1,510
Jan. 14....	531.8	38	4.2	23	243	23.7	52.9	(.70)	8,700	8,200	1,590
Apr. 18....	605.6	42	12.6	20	28	25.4	79.6	.89	10,700	8,800	1,800
Apr. 19....	593.6	38	6.0	20	51	23.9	59.5	.82	8,600	7,200	1,470
Apr. 20....	581.0	38	7.2	20	75	21.4	56.0	(.73)	8,800	7,600	1,530
Apr. 21....	571.4	38	2.4	15	99	19.3	52.4	.73	8,300	7,300	1,450
Apr. 22....	567.0	34	3.2	20	123	19.7	51.6	.73	8,100	7,100	1,420
Apr. 23....	565.2	30	4.2	22	144	23.3	51.8	[.70]	8,500	7,500	1,500
Apr. 24....	557.2	30	3.8	22	171	22.9	48.0	(.70)	7,900	7,100	1,410
Apr. 25....	552.8	32	3.6	22	195	23.4	51.1	(.70)	8,400	7,600	1,500
Apr. 26....	548.6	34	4.0	23	219	24.3	51.1	(.70)	8,400	7,700	1,510
Apr. 27....	545.6	32	4.8	20	243	19.9	47.6	(.70)	7,800	7,100	1,410
Apr. 28....	541.6	30	2.0	22	267	20.8	45.9	(.70)	7,500	6,900	1,360
Apr. 29....	535.4	32	3.0	21	291	22.1	46.9	.70	7,700	7,200	1,400
Apr. 30....	531.2	32	3.6	21	312	22.3	44.9	(.70)	7,300	6,900	1,340
May 1....	529.4	30	3.4	21	336	22.4	43.6	(.70)	7,100	6,700	1,300
June 2	602.0	40	10.8	23	22	26.0	80.6	.85	11,300	9,400	1,920
June 3....	584.2	40	5.2	22	46	23.4	63.8	.75	9,800	8,400	1,690
June 4....	567.6	44	5.6	23	67	25.7	52.6	.73	8,300	7,300	1,460
June 5....	558.2	32	4.6	25	94	26.6	52.4	.70	8,600	7,700	1,530
June 7....	548.2	32	7.8	26	143	29.0	53.9	[.70]	8,800	8,000	1,580
Nov. 7....	672.4	48	12.6	....	26	25.4	[1]84.3	.74	[1]13,200	[1]9,800	[1]2,090
Nov. 8..	654.4	38	7.8	....	50	24.3	[1]72.6	.76	[1]11,100	[1]8,500	[1]1,780
Nov. 9....	651.6	44	8.0	....	73	26.7	[1]66.4	.73	[1]10,500	[1]8,100	[1]1,690
Nov. 10....	638.6	40	7.2	....	98	26.4	[1]58.1	(.72)	[1]9,300	[1]7,300	[1]1,520
Nov. 11....	631.2	40	3.0	....	122	16.8	[1]59.8	.72	[1]9,400	[1]7,400	[1]1,550
Nov. 14....	625.0	36	2.0	....	192	13.4	58.5	[.70]	9,600	7,700	1,590
Nov. 15....	617.2	38	4.0	....	218	27.8	61.9	[.70]	10,100	8,200	1,680
1923											
Jan. 4....	686.2	38	6.4	6	25	6.3	66.6	.83	9,500	6,900	1,480
Jan. 5....	683.0	36	3.0	9	49	7.7	59.2	.73	9,300	6,800	1,460
Jan. 6....	680.4	36	2.8	12	73	9.6	55.3	.72	8,800	6,500	1,380
Jan. 22....	686.4	40	10.8	28	25	26.7	56.9	.83	8,100	5,900	1,260
Jan. 22....	686.4	36	10.8	28	30	27.9	56.8	.83	8,100	5,900	1,260
Jan. 23....	683.0	34	4.4	7	49	−1.9	62.8	.76	9,600	7,000	1,500
Jan. 29....	694.2	40	4.8	8	25	2.9	77.8	.82	11,200	8,100	1,740
Jan. 30....	691.4	36	5.0	25	49	24.9	43.1	.73	6,800	4,900	1,060
Feb. 6....	693.2	42	5.2	6	25	2.6	67.2	.83	9,600	6,900	1,490
Feb. 7....	691.0	34	2.8	5	49	2.0	65.9	.73	10,400	7,500	1,610

[1] Steer standing and lying.

TABLE 44.—*Metabolism of steer C when fasting at different levels of nutrition*—Continued

Date	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Hours without food to beginning of experiment	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours		
									Total	Per 500 kg.	Per sq. m.
1923	*kg.*		*kg.*	*°C.*		*°C.*	*gm.*		*cal.*	*cal.*	*cal.*
eb. 12....	689.6	35	4.6	8	25	3.9	69.8	0.84	9,800	7,100	1,520
eb. 13....	686.6	40	2.8	8	49	1.7	61.7	.74	9,600	7,000	1,500
eb. 19....	689.8	40	3.4	4	25	2.5	74.6	.82	10,700	7,800	1,660
eb. 20....,	687.2	42	3.6	0	49	−1.0	73.0	.70	11,900	8,700	1,860
ar. 2....	694.8	40	6.2	12	25	7.3	73.2	.83	10,400	7,500	1,610
ar. 3....	692.4	48	3.8	14	49	10.9	59.3	.79	8,800	6,400	1,370
ar. 9....	694.0	34	4.6	4	25	4.3	71.8	.84	10,100	7,300	1,570
ar. 10....	691.8	36	3.0	6	49	2.0	69.0	.77	10,400	7,500	1,610
ar. 16....	698.6	42	5.2	8	26	11.9	71.9	.80	10,500	7,500	1,620
ar. 17....	695.6	34	3.2	8	50	24.4	58.7	.77	8,900	6,400	1,380
ar. 23....	681.4	40	14.8	26	25	29.2	80.5	.86	11,200	8,200	1,760
ar. 24....	676.8	40	8.8	22	49	13.5	65.2	.79	9,700	7,200	1,530
ov. 6....	694.0	46	6.2	....	42	21.5	81.7	.79	12,100	8,700	1,880
ov. 7....	675.8	44	3.8	....	65	18.3	67.7	.74	10,600	7,800	1,670
ov. 8....	665.2	48	3.0	....	89	18.5	59.3	.73	9,400	7,100	1,500
ov. 9 ..	656.4	40	2.8	....	113	22.6	62.5	.72	10,000	7,600	1,610
ov. 10....	(656.4)	34	....	....	137	22.5	63.5	.70	10,400	7,900	1,670
1924											
ar. 4....	636.6	36	....	14	27	12.0	55.1	.82	7,900	6,200	1,290
ar. 5....	627.2	30	1.4	16	49	11.1	42.8	.74	6,700	5,300	1,110
ar. 6....	619.6	40	2.6	16	73	15.2	43.8	.71	7,100	5,700	1,180
r. 7....	613.4	28	1.8	16	98	13.1	44.4	.70	7,300	6,000	1,220
r. 8....	609.8	28	1.4	14	122	12.3	44.5	.70	7,300	6,000	1,230
r. 9....	604.8	24	3.8	16	146	21.3	44.2	.71	7,100	5,900	1,200
r. 10....	600.4	25	2.0	18	170	17.7	45.8	.70	7,500	6,200	1,270
r. 11....	597.0	28	2.2	14	195	10.7	44.9	.70	7,300	6,100	1,240
r. 12....	593.8	24	2.2	16	219	14.0	44.7	.71	7,200	6,100	1,230
r. 13....	589.6	34	2.0	16	241	17.5	40.7	.70	6,700	5,700	1,150
v. 13[2] ...	764.2	54	9.2	....	45	24.4	[1]77.9	.76	[1]11,900	[1]7,800	[1]1,740

[1] Steer standing and lying.

[2] Steer not in normal condition; vomited while in respiration chamber.

measurement of the gaseous metabolism. The average chamber temperature indicates the temperature existing during the 3 or 4 half-hour periods when the animal was inside the respiration chamber. The actual number of hours elapsing between the last ingestion of food and the beginning of the respiration experiment is given for each date, rather than the number of days that the animal had been fasting.

The respiratory quotients in the fasts in April 1922 and in the subsequent fasts were usually actually determined with the Carpenter gas-analysis apparatus, but no determinations were made for the fasts in December 1921 and January 1922, and respiratory quotients had to be assumed in these cases. All respiratory quotients not actually determined but assumed are inclosed in parentheses. Those inclosed in square brackets are based upon quotients which were actually determined but which were somewhat below 0.70, and for purposes of computing the heat-production a quotient of 0.70 has been assumed in these cases. Since the fasts of steers C and D in December 1921 and January 1922 were made at a maintenance level of

Table 45.—*Metabolism of steer D when fasting at different levels of nutrition*

Date	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Hours without food to beginning of experiment	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours		
									Total	Per 500 kg.	Per sq. m.
	kg.		*kg.*	°*C.*		°*C.*	*gm.*		*cal.*	*cal.*	*cal.*
1921											
Dec. 7....	601.4	36	4.4	5	30	22.0	85.6	(0.82)	12,300	10,200	2,080
Dec. 8....	582.6	36	3.2	5	54	19.9	63.8	(.76)	9,700	8,300	1,680
Dec. 9....	576.4	36	3.2	15	78	22.3	61.3	(.73)	9,700	8,400	1,690
Dec. 10....	576.8	36	3.8	20	99	23.7	58.1	(.72)	9,300	8,100	1,620
Dec. 11....	569.8	....	3.6	18	123	23.4	56.1	(.71)	9,100	8,000	1,600
Dec. 12....	563.6	....	2.4	17	148	23.1	54.1	(.70)	8,800	7,900	1,550
Dec. 13....	566.6	....	3.4	20	172	25.6	53.0	(.70)	8,700	7,700	1,530
1922											
Jan. 5....	607.0	48	11.4	20	29	22.7	84.9	(.82)	12,200	10,000	2,060
Jan. 6....	593.6	40	7.0	20	53	21.2	67.3	(.76)	10,300	8,700	1,760
Jan. 7....	591.2	40	5.0	20	77	21.9	60.3	(.73)	9,500	8,000	1,630
Jan. 8....	578.8	38	6.8	21	99	24.5	56.3	(.72)	9,000	7,800	1,560
Jan. 9....	586.2	36	5.2	24	125	23.6	56.3	(.71)	9,100	7,800	1,570
Jan. 10....	578.0	32	4.0	20	149	21.7	52.4	(.70)	8,600	7,400	1,500
Jan. 11....	578.4	36	3.0	20	173	23.0	53.9	(.70)	8,800	7,600	1,530
Jan. 12....	571.0	36	4.0	21	197	23.7	49.6	(.70)	8,100	7,100	1,420
Jan. 13....	568.0	28	4.4	23	221	22.4	50.6	(.70)	8,300	7,300	1,460
Jan. 14....	570.4	27	4.0	23	245	23.4	51.3	(.70)	8,400	7,400	1,470
Apr. 18....	621.0	40	12.4	20	32	25.8	83.4	.97	10,500	8,500	1,740
Apr. 19....	608.6	36	4.2	20	56	24.5	67.8	.83	9,700	8,000	1,630
Apr. 20....	599.4	34	5.2	20	80	22.0	59.5	.75	9,200	7,700	1,560
Apr. 21....	593.4	42	4.2	20	104	20.1	54.4	.75	8,400	7,100	1,440
Apr. 22....	586.6	42	3.0	15	128	21.6	53.0	.74	8,300	7,100	1,430
Apr. 23....	585.8	38	3.8	20	146	24.0	51.9	.73	8,200	7,000	1,410
Apr. 24....	578.8	32	3.6	22	173	24.1	50.8	(.72)	8,100	7,000	1,410
Apr. 25....	578.6	38	3.8	22	200	24.3	51.0	(.71)	8,200	7,100	1,420
Apr. 26....	575.6	30	4.6	22	221	26.5	49.8	(.70)	8,100	7,000	1,410
Apr. 27....	571.8	36	3.4	23	245	21.0	47.4	(.70)	7,800	6,800	1,360
Apr. 28....	565.0	36	3.2	20	272	20.3	51.0	(.70)	8,300	7,300	1,460
Apr. 29....	563.8	32	2.8	22	296	24.1	48.0	(.70)	7,900	7,000	1,390
Apr. 30....	557.2	34	4.2	21	315	23.0	47.5	(.70)	7,800	7,000	1,390
May 1....	551.8	32	2.8	21	339	24.1	47.4	(.70)	7,800	7,100	1,400
June 2....	610.8	54	9.2	23	31	27.3	83.7	.77	12,700	10,400	2,130
June 3....	593.0	52	6.2	22	55	25.8	67.7	.73	10,700	9,000	1,830
June 4....	585.8	48	6.2	23	74	28.8	64.1	.70	10,500	9,000	1,810
June 5....	575.4	48	5.2	25	103	31.5	57.5	.71	9,300	8,100	1,620
June 6....	577.8	46	8.0	27	121	29.0	61.2	[.70]	10,000	8,700	1,740
Nov. 8....	661.2	48	9.4	....	54	26.4	80.7	.72	12,900	9,800	2,060
Nov. 9....	649.8	48	8.8	....	78	26.7	71.3	.71	11,500	8,800	1,860
Nov. 10....	640.4	48	8.6	....	102	26.5	69.8	(.71)	11,300	8,800	1,840
Nov. 12....	645.0	42	3.0	....	144	16.2	63.1	(.70)	10,300	8,000	1,670
Nov. 13....	638.6	40	2.6	....	168	9.3	60.0	(.70)	9,800	7,700	1,600
1923											
Jan. 10....	688.6	48	6.4	13	26	7.0	79.6	.83	11,300	8,200	1,760
Jan. 11....	685.8	42	3.4	9	49	7.0	64.8	.73	10,200	7,400	1,590
Jan. 12....	683.8	38	3.0	10	74	2.7	54.5	.70	8,900	6,500	1,390
Jan. 18....	690.0	42	6.0	12	25	3.4	76.5	.81	11,100	8,000	1,730
Jan. 19....	686.2	48	8.2	28	49	28.2	53.1	.74	8,300	6,000	1,290
Jan. 26....	688.6	44	5.8	11	26	8.8	82.6	.82	11,900	8,600	1,850
Jan. 27....	685.8	38	6.8	26	49	28.3	50.8	.78	7,600	5,500	1,190
Feb. 2....	681.4	44	6.0	23	25	27.9	74.0	.86	10,300	7,600	1,610
Feb. 3....	677.4	40	3.4	12	47	7.3	59.6	.75	9,200	6,800	1,450
Feb. 9....	686.4	40	5.0	8	25	8.6	75.6	.78	11,300	8,200	1,760
Feb. 10....	683.0	42	3.2	10	49	5.7	67.3	.77	10,200	7,500	1,600
Feb. 15....	695.4	40	4.6	− 3	25	−1.6	83.6	.82	12,000	8,600	1,860
Feb. 16....	691.0	76	2.2	− 3	49	−7.5	85.6	.75	13,200	9,600	2,050

TABLE 45.—*Metabolism of steer D when fasting at different levels of nutrition*—Continued

Date	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Hours without food to beginning of experiment	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours.		
									Total	Per 500 kg.	Per sq. m.
1923	*kg.*		*kg.*	°*C.*		°*C.*	*gm.*		*cal.*	*cal.*	*cal.*
Feb. 23....	691.4	54	4.4	+ 2	25	3.6	79.8	.83	11,400	8,200	1,770
Feb. 24....	688.4	48	3.2	− 2	49	0.2	73.7	.73	11,600	8,400	1,810
Mar. 6....	690.6	64	3.8	4	25	2.1	80.2	.83	11,400	8,300	1,770
Mar. 7....	687.6	44	3.8	3	50	0.3	75.1	(.75)	11,600	8,400	1,810
Mar. 14...	695.4	48	6.0	7	25	10.5	79.7	.84	11,200	8,100	1,730
Mar. 15...	692.6	38	3.8	5	50	22.8	72.3	.79	10,700	7,700	1,660
Mar. 21....	693.2	52	14.2	24	26	12.6	83.7	.86	11,600	8,400	1,800
Mar. 22....	688.4	38	10.4	27	49	29.0	68.0	.76	10,400	7,600	1,620
Nov. 5....	707.0	60	....	....	22	22.1	117.4	.86	16,300	12,000	2,490
Nov. 6....	669.6	72	11.6	....	46	21.2	86.2	.76	13,200	9,900	2,090
Nov. 7. ..	653.6	52	5.0	....	70	19.9	71.4	.72	11,400	8,700	1,830
Nov. 8....	658.8	52	4.8	....	94	15.2	70.4	.72	11,200	8,500	1,790
Nov. 9....	651.4	64	4.0	....	116	23.2	62.9	.71	10,200	7,800	1,650
1924											
Mar. 4....	624.0	44	....	14	32	13.6	67.9	.73	10,700	8,600	1,770
Mar. 5....	610.0	32	3.4	16	52	14.9	59.3	.73	9,400	7,700	1,580
Mar. 6....	602.2	32	2.8	16	77	15.9	53.8	.70	8,800	7,300	1,490
Mar. 7....	606.4	36	2.8	16	102	11.9	53.0	.70	8,700	7,200	1,470
Mar. 8....	598.8	48	2.2	14	126	11.7	49.5	(.70)	8,100	6,800	1,380
Mar. 9....	593.4	50	2.8	16	149	19.3	55.7	(.70)	9,100	7,700	1,560
Mar. 10....	596.4	34	4.0	18	174	15.6	51.4	.70	8,400	7,000	1,430
Mar. 11....	590.6	36	2.2	14	198	13.8	44.3	.70	7,200	6,100	1,230
Mar. 12....	587.2	34	1.4	16	228	16.2	45.0	.71	7,300	6,200	1,260

TABLE 46.—*Metabolism of steers E and F when fasting after submaintenance feeding*

Steer and date (1924)	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Hours without food to beginning of experiment	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours		
									Total	Per 500 kg.	Per sq. m.
teer E:	*kg.*		*kg.*	°*C.*		°*C.*	*gm.*		*cal.*	*cal.*	*cal.*
Feb. 13...	247.4	40	3.0	16	27	15.5	38.0	0.84	5,400	10,900	1,600
Feb. 14...	238.6	36	1.8	15	51	14.7	35.0	.72	5,600	11,700	1,690
Feb. 15...	235.0	34	2.0	16	75	17.6	30.9	[.70]	5,100	10,900	1,550
Feb. 16...	234.0	36	2.6	15	98	14.6	31.7	[.70]	5,200	11,100	1,590
teer F:											
Feb. 13...	273.0	40	3.8	16	32	17.4	37.5	.78	5,600	10,300	1,560
Feb. 14...	263.0	36	1.2	15	55	17.0	36.4	.73	5,700	10,800	1,620
Feb. 15...	257.4	38	2.2	16	79	19.0	36.1	[.70]	5,900	11,500	1,700
Feb. 17...	254.2	34	2.2	14	122	21.1	33.9	.72	5,400	10,600	1,570

nutrition, the assumptions for the respiratory quotients used in computing the heat-production for these fasts were based upon respiratory quotients obtained during the fasts in April and June 1922 and the series of short fasts in 1923, all of which also followed maintenance feeding.

The computations of the heat-production were carried out as described on page 148, the values for the body-surface being derived from the curve given in Fig. 8, page 155.

The feed-level prior to each of the fasts reported in Tables 44, 45, and 46 has been indicated in Table 47. The last individual feed before each fast is given in Table 11, page 53.

TABLE 47.—*Feed-level prior to long and short fasts*

Steer and dates	Per day	
	Hay	Meal
	kg.	*kg.*
Steers C and D:		
Nov. 26, 1921 to Dec. 6, 1921[1]	9.0	1.36
Dec. 27, 1921 Jan. 4, 1922	7.5	6.00
Mar. 31, 1922 Apr. 17, 1922	9.0	3.00
May 9, 1922 June 1, 1922	9.0	4.00
June 10, 1922 Nov. 6, 1922	Pasture	
Nov. 20, 1922 Mar. 27, 1923	9.0	2.00
June 23, 1923 Nov. 4, 1923	Pasture	
Dec. 21, 1923 Mar. 3, 1924	4.5	....
Steer C:		
May 19, 1924 Nov. 11, 1924	Pasture	
Steers E and F:		
Dec. 18, 1923 Feb. 12, 1924	2.5	[2]0.30

[1] Steers C and D were purchased Oct. 26, 1921; fed hay *ad libitum* and 3 kg. meal until Nov. 26, 1921.

[2] Meal ration reduced to 100 gm. on Jan. 28, 1924.

This tabular presentation of the data secured in the series of long and short fasts is specifically for the purpose of accurate recording of results. The large number of experiments and the length of the tables make discussion of each individual experiment based upon these tables somewhat difficult. For this reason only the most general features will be brought out at this point, and the more critical discussion will be based upon the values for heat-production, which will be summarized in tabular form to show the course of the metabolism during each fast and which will enable the comparison of one fast with another and of one animal with another (see Tables 48 to 51, pp. 173 to 181).

A general inspection of Tables 44, 45, and 46 shows that as the fast progresses there is a decrease in all the factors measured, the live weight, the heart-rate, the insensible perspiration, the carbon-dioxide production, the respiratory quotient, and also the computed heat-production.

The fasts varied in one striking particular, that is, in the previous state of nutrition of the animal. Thus, the two November fasts of steers C and D followed pasture feeding, the fasts in March 1924, with steers C and D, and in February 1924, with steers E and F, followed submaintenance feeding, and all of the other fasts followed essentially maintenance feeding. In most of the fasts of 5 to 14 days' duration the chamber temperature did not undergo extreme changes during any one fast. The range in temperatures was from about 15° to 30° C., but a large proportion of the experiments were made at about 20° C. Occasionally low temperatures are recorded, however, as, for instance, on November 13, 1922, with steer D. In the series of short fasts in 1923 pronounced differences in the temperature of the chamber were designedly made. In any consideration of the figures, therefore, one must continually bear in mind the environmental temperature at which the experiments were made and particularly the previous state of nutrition of the animals.

The two large, mature animals, C and D, were subjected to exactly the same conditions as to previous state of nutrition and environmental temperature, in order that they might be as nearly as possible physiological duplicates, as were steers A and B in our earlier study of undernutrition. To introduce the factor of immaturity and growth, the two younger and smaller steers, E and F, were studied. Obviously, a direct comparison can not be made between the values obtained with these two steers and those obtained with steers C and D without taking into consideration not only the previous state of nutrition and the environmental temperature, but likewise the age and weight of the animals.

Course of the Heat-production During Fasts of 5 to 14 Days, at Different Levels of Nutrition

The chief index of vital activity and the one factor above all others which one would expect to be affected by the lack of food is the general metabolism, particularly the heat-production. The excretion of carbon dioxide and certain physiological factors, such as heart-rate and respiration-rate, have already been considered in a general way. The clearest cut evidence as to the degree of vital activity, however, is to be found in the computed heat-production. The data for the fasting experiments permit treatment in a variety of ways. If only one fasting experiment had been made, this would be considered from every angle. But the treatment of so many fasting experiments seems to be best made by a critical study of the computed heat values alone. The data for all of the longer fasts will accordingly be considered at the same time. The heat values have been computed upon three bases: (1) the total heat-production per 24 hours, computed from the average of 3 or 4 half-hour carbon-dioxide measurements each morning; (2) the heat-production per 500 kg. of body-weight per 24 hours; and (3) the heat-production per square meter of body-surface per 24 hours.

TOTAL HEAT-PRODUCTION PER 24 HOURS

The total daily heat-production for each day of the fasts of 5 to 14 days is presented in Table 48 for all four animals. Owing to the fact that the two animals in each pair fasted during the same periods, it was impossible to make the respiration experiments with both animals at the same time of day. Thus, steer C was usually studied first in the respiration chamber and steer D immediately afterwards, and the same treatment was accorded to steers E and F. In Table 48, therefore, in addition to the record of the number of days that the animal had been fasting, the number of hours after food when the respiration experiment was made is also indicated for each day. Thus, the respiration experiments on the first day of fasting began with all animals between the twenty-second and thirty-second hour after food was withdrawn. This time interval is such that these experiments on the first day represent the so-called "standard metabolism" experiments with steers, since in all but one instance the animals were standing during the period of measurement. Standard metabolism measurements were also secured with these animals from time to time throughout the entire period of their study, and further reference will be made later to the data reported for the first day of fasting in Table 48, when the standard metabolism experiments as a whole are considered. (See pp. 228 to 230.)

The consideration of the total heat-production per 24 hours, irrespective of the size of the animal, its previous state of nutrition, and the environmental temperature to which it has been exposed, precludes immediately any exact comparison of the different fasts with each other, and greatest stress must therefore be laid upon the metabolism during the successive days of any given fast. It is first to be observed that there is immediately a rapid decrease in the metabolism, which continues as the fast progresses, being roughly proportional to the length of the fast. Thus, in the 14-day fast in April 1922, with steer D the heat-production dropped from 10,500 calories on the first day to 7,800 calories on the fourteenth day, a fall of 2,700 calories per 24 hours. An even greater fall was noticed in 4 days in the June 1922 fast with this same animal, however, from 12,700 to 9,300 calories on the fourth day, or a drop of 3,400 calories.

The largest decrease in the heat-production is usually found between the first and the second day, and this is undoubtedly immediately incidental to the withholding of food. This is strikingly shown in the November 1923 fast with steer D, when the heat-production fell from 16,300 calories on the first day to 13,200 calories on the second day, a fall of 3,100 calories. After the second day, however, the decrease is for the most part regular in each individual fast, and the total decrease is greater the longer the fast.

Although there are differences in the average level of metabolism in the different fasts, it is only in the fast in March 1924 that such a pronounced difference in metabolic level is found as to challenge attention. Indeed, the metabolism, particularly toward the end of this fast with both steer C and steer D, is altogether different from that at the end of any of the other fasts of essentially the same length. Thus, the lowest value found with steer C prior to March 1924 was 7,100 calories on the fourteenth day of the April fast, and yet this value is actually higher than that measured on the second day of the fast in March 1924. With steer D the lowest value found prior to the March fast, namely, 7,800 calories, occurred on the tenth, thirteenth, and fourteenth days of the April fast, and yet this is larger than the values found on the eighth and ninth days of the fast in March 1924. Further discussion of the fast in March 1924 will be entered into later, and it need only be pointed out here that this fast followed pronouncedly submaintenance rations. Incidentally it should also be added that the November fasts, both in 1922 and 1923, with both animals, followed pasture feeding. As has been frequently stated in the text, steers E and F were younger and smaller than the mature animals, and hence their seemingly very low heat-production of between 5,100 and 5,900 calories is explained by this fact as well as by the fact that their fasts likewise followed submaintenance feeding.

TABLE 48.—*Heat-production per 24 hours during fasts of 5 to 14 days*

Steer and dates of fasts	Days fasting													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	Hours without food													
	22 to 32	42 to 56	65 to 80	89 to 104	113 to 128	137 to 149	168 to 174	192 to 200	216 to 228	241 to 245	267 to 272	291 to 300	312 to 315	336 to 339
Steer C:	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*
Dec. 6 to 13, 1921	10,900	9,500	8,700	8,400	8,300	8,200	8,100	......	......	......	......	......	......	......
Jan. 4 14, 1922	11,400	10,800	9,600	8,400	8,900	8,400	8,400	7,700	8,300	8,700	......	......	......	......
Apr. 17 May 1, 1922	10,700	8,600	8,800	8,300	8,100	8,500	7,900	8,400	8,400	7,800	7,500	7,700	7,300	7,100
June 1 7, 1922	11,300	9,800	8,300	8,600	......	8,800	......	......	......	......	......	......	......	......
Nov. 6 16, 1922	[1] 13,200	[1] 11,100	[1] 10,500	[1] 9,300	[1] 9,400	......	......	9,600	10,100	......	......	......	......	......
Nov. 4 10, 1923	(2)	12,100	10,600	9,400	10,000	10,400	......	......	......	......	......	......	......	......
Mar. 3 13, 1924	7,900	6,700	7,100	7,300	7,300	7,100	7,500	7,300	7,200	6,700	......	......	......	......
Steer D:														
Dec. 6 to 13, 1921	12,300	9,700	9,700	9,300	9,100	8,800	8,700	......	......	......	......	......	......	......
Jan. 4 14, 1922	12,200	10,300	9,500	9,000	9,100	8,600	8,800	8,100	8,300	8,400	......	......	......	......
Apr. 17 May 1, 1922	10,500	9,700	9,200	8,400	8,300	8,200	8,100	8,200	8,100	7,800	8,300	7,900	7,800	7,800
June 1 6, 1922	12,700	10,700	10,500	9,300	10,000	......	......	......	......	......	......	......	......	......
Nov. 6 14, 1922	......	12,900	11,500	11,300	......	10,300	9,800	......	......	......	......	......	......	......
Nov. 4 9, 1923	16,300	13,200	11,400	11,200	10,200	......	......	......	......	......	......	......	......	......
Mar. 3 12, 1924	10,700	9,400	8,800	8,700	8,100	9,100	8,400	7,200	7,300	......	......	......	......	......
Steer E:														
Feb. 12 to 17, 1924	5,400	5,600	5,100	5,200	......	......	......	......	......	......	......	......	......	......
Steer F:														
Feb. 12 to 18, 1924	5,600	5,700	5,900	......	5,400	......	......	......	......	......	......	......	......	......

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[1] Measurement made during period of lying and standing.

[2] A 24-hour heat-production of 16,400 calories was noted when the steer had been 18 hours without food.

The pronounced influence of the previous state of nutrition upon the fasting metabolism is thus clearly indicated, not only by the falling off in the metabolism during each day of the fast (because the previous store of food is depleted more and more as time goes on) but by the general level of the fasting metabolism, which is strikingly lower in the fasts following submaintenance feeding. In the case of the two smaller animals, however, this effect is not to be observed from Table 48 alone, but can only be noted when a comparison is made between their fasting metabolism at the submaintenance level and their standard metabolism following maintenance feeding. (See p. 232.)

Average figures can not be drawn from the values given in Table 48 for the total 24-hour heat-production, since all the animals were changing in weight, the previous states of nutrition were markedly different in the different fasts, and the environmental temperature was in some cases changed unintentionally and in other cases it was purposely altered to study the influence of this factor upon metabolism. The general conclusions to be drawn, however, are that there is a rapid and persistent decrease in the heat-production of these large ruminants during fasting, and that the previous state of nutrition, particularly when a submaintenance ration has been given, has a pronounced influence upon the fasting metabolism in that the metabolism begins at a much lower level than in the other cases and falls to a still lower level as the fast progresses. Finally, the same mature animal within a period of two years may have markedly different fasting levels, even if the fast following submaintenance feeding is excepted.

HEAT-PRODUCTION PER 500 KG. OF BODY-WEIGHT PER 24 HOURS

The heat-production of these steers during the fasts of 5 to 14 days has also been computed on the basis of 500 kg. of body-weight,[a] and the values are given in Table 49, in which the days of fasting correspond exactly to those reported in Table 48. By this method of computation the differences in the size of the animal as any one fast progresses and the differences in the size of the same animal from year to year are taken into account, and it is permissible not only to consider the data from the standpoint of the consecutive days of fasting, but likewise to compare the results obtained in the various fasts and with the different animals. The results confirm the findings noted in the analysis of the data for the 24-hour heat-production, namely, that in spite of the changes in body-weight, the metabolism distinctly decreases during the fast, and that usually the lowest values appear at the end of the longer fasts.

The lowest value found with steer C outside of the fast in March 1924, namely, 6,700 calories, occurred (as in the case of the total heat-production) on the fourteenth day of fasting. Although there is some variability

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[a] It is particularly to be emphasized that in this report the calculations of the heat-production per 500 kg. of body-weight are derived by referring the weight of the animal by direct proportion to a standard weight of 500 kg. and not to the two-thirds power of the weight, which is frequently done by other writers. Obviously, the heat-production computed per 500 kg. of body-weight has the same significance as the heat-production per kilogram of body-weight, so commonly computed for man and other animals. But it seems best to refer the heat-production of these large animals to the approximate average weight of a mature steer, i. e., 500 kg.

in the values, there is with this animal a clear-cut picture of a continually falling metabolism, especially during the 14-day fast. In the fast in March 1924, much lower values are noted than in any of the other fasts. The body-weight was lower at this time, but the computation of the heat-production per 500 kg. of body-weight eliminates to a certain extent any differences due to differences in body-weight, and it is thus evident that the low metabolic level noted in this March fast reflects the influence of the preceding submaintenance régime.

In the fasts following maintenance feeding, that is, in the first six fasts with each of the larger animals, the fasting metabolism reaches a reasonably constant level on or about the fourth or the fifth day, but it can not be definitely asserted that on any certain day the metabolism had reached a minimum point with either animal in all experiments. This may be in part due to the fact that although the animals were measured in the standing position, the activity while the animal was inside the respiration chamber differed somewhat from day to day. It is believed, however, that the irregularities in metabolism can by no means be wholly explained by differences in activity during the respiration experiment. The graphic records show, it is true, variations in the activity when the animal was inside the chamber and indicate that there was a general tendency, although by no means uniform, for the animals to be less active as the fast progressed. A part of the fall in metabolism shown in Table 49 may therefore be due to a greater degree of repose. Variability in activity is one of the great stumbling blocks in the study of the metabolism of these animals, whose activity can not be controlled. It is a distinct argument in favor of the 24-hour experiment, in which the uniformity in stall activity would be greater in general than in any chance three or four consecutive half-hour periods. Indeed, at this stage of our experimentation we were inclined to believe that the 24-hour period would enormously help in the explanation of these figures. But even in 24-hour experiments irregularity in activity occurs persistently, although in general the animals lie down a little longer as the fast progresses. Since the experiments reported in Table 49 comprised three or four consecutive half-hour periods inside the respiration chamber, and the steer was always forced to stand during these short experiments, the chamber activity was for the most part of sufficient relative uniformity so that the differences could not wholly explain the differences in the metabolism noted in this table.

A second factor which is known to influence the metabolism of animals is that of environmental temperature. The uniformity in the environmental temperature in these experiments was by no means so great as it should have been. This is particularly true in the two experiments in December 1921, as can be seen by reference to Tables 44 and 45 (pp. 166 and 168). Thus, on the two days preceding the metabolism measurements, the stall temperature for 24 hours was low, 5° C., but the chamber temperatures during the experiment were higher, i. e., from 17° to 22° C. In the other long fasts, however, there was not such a marked difference between the stall temperature preceding and the chamber temperature during the experiment.

TABLE 49.—*Heat-production per 500 kg. of body-weight per 24 hours during fasts of 5 to 14 days*

Steer and dates of fasts	Days fasting													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	Hours without food													
	22 to 32	42 to 56	65 to 80	89 to 104	113 to 128	137 to 149	168 to 174	192 to 200	216 to 228	241 to 245	267 to 272	291 to 300	312 to 315	336 to 339
Steer C:	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*
Dec. 6 to 13, 1921...	9,300	8,500	7,900	7,700	7,600	7,600	7,600	....	....	......	......	......	......	......
Jan. 4 14, 1922...	9,700	9,500	8,500	7,600	8,100	7,700	7,800	7,200	7,700	8,200	......	......	......	......
Apr. 17 May 1, 1922	8,800	7,200	7,600	7,300	7,100	7,500	7,100	7,600	7,700	7,100	6,900	7,200	6,900	6,700
June 1 7, 1922...	9,400	8,400	7,300	7,700	....	8,000	....	....	....	......	......	......	......	......
Nov. 6 16, 1922...	[1]9,800	[1]8,500	[1]8,100	[1]7,300	[1]7,400	....	....	7,700	8,200	......	......	......	......	......
Nov. 4 10, 1923...	(2)	8,700	7,800	7,100	7,600	7,900	....	....	....	......	......	......	......	......
Mar. 3 13, 1924...	6,200	5,300	5,700	6,000	6,000	5,900	6,200	6,100	6,100	5,700	......	......	......	......
Steer D:														
Dec. 6 to 13, 1921...	10,200	8,300	8,400	8,100	8,000	7,900	7,700	....	....	......	......	......	......	......
Jan. 4 14, 1922...	10,000	8,700	8,000	7,800	7,800	7,400	7,600	7,100	7,300	7,400	......	......	......	......
Apr. 17 May 1, 1922	8,500	8,000	7,700	7,100	7,100	7,000	7,000	7,100	7,000	6,800	7,300	7,000	7,000	7,100
June 1 6, 1922...	10,400	9,000	9,000	8,100	8,700	....	....	....	....	......	......	......	......	......
Nov. 6 14, 1922...	....	9,800	8,800	8,800	....	8,000	7,700	....	....	......	......	......	......	......
Nov. 4 9, 1923...	12,000	9,900	8,700	8,500	7,800	....	....	....	....	......	......	......	......	......
Mar. 3 12, 1924...	8,600	7,700	7,300	7,200	6,800	7,700	7,000	6,100	6,200	......	......	......	......	......
Steer E:														
Feb. 12 to 17, 1924...	10,900	11,700	10,900	11,100	....	....	....	....	....	......	......	......	......	......
Steer F:														
Feb. 12 to 18, 1924....	10,300	10,800	11,500	....	10,600	....	....	....	....	......	......	......	......	......

[1] Measurement made during period of lying and standing.

[2] A 24-hour heat-production of 11,300 calories per 500 kg. of body-weight was noted when the steer had been 18 hours without food.

Indeed, the changes in temperature from day to day during these fasting experiments were, for the most part, very small, so that any great change in the metabolism can not, save possibly in the first experiment, be attributed to the environmental temperature. The average environmental temperature during most of the fasts was about 20° C. In the March fasts perceptibly lower temperatures prevailed and in the June fasts perceptibly higher temperatures. It is obvious that the temperature of the chamber during an experiment made in June would be higher than that during an experiment made in January of the same year. Thus, the chamber temperatures during the fasts in June 1922 were from 26° to 28° C. The values for the heat-production per 500 kg. of body-weight, however, are not appreciably lower in the June fast of steer C than in the other fasts with this animal. They are somewhat lower, for the most part, than the values in the January fast, but they are higher than those in the April fast. In the case of steer D the reverse is true, that is, the June values are actually higher than those in January. In fact, the highest values in the series up to that date were found in June 1922.

In the earlier research on undernutrition in steers it was noted that the effect of environmental temperature seemed to be small and was contrary to the commonly accepted belief that the lower temperature is accompanied by a higher metabolism in warm-blooded animals. Indeed, certain of the results obtained suggested strongly that the metabolism may be lower the lower the temperature. The necessity for constancy in environmental temperature was therefore not stressed perhaps as much as it should have been in these fasting experiments of 5 to 14 days. Subsequently, however, a special study of the influence of environmental temperature was made in a series of short fasts in 1923 (see pp. 180 to 185) and in a series of 4-day experiments with steers E and F (see pp. 200 to 202). As no irritating agencies pestering the animals could be accounted for, the difference in the heat-production in this series of fasts must be ascribable to true cell differences in the metabolism of these animals at different stages and is not due to differences either in abnormal stall activity or in environmental temperature. The preceding nutritive state, however, particularly the submaintenance level of nutrition, did have an influence.

Although it was noted in Table 48 that steers E and F had a much lower total heat-production on the different days of their fasts than did steers C and D, the calculations on the basis of equal body-weight, reported in Table 49, show that these animals actually had a higher metabolism per 500 kg. of body-weight than did the adult animals, especially after the first day. The metabolism of steers E and F was higher even when their fasting values after submaintenance feeding are compared with those for steers C and D in the fasts after maintenance feeding. Indeed, on no day was the heat-production of steer F per 500 kg. of body-weight lower than 10,300 calories. This evidence is, in all probability, to be taken as an index of the greater activity of the younger protoplasm, and it is fully in line with the finding on humans that the heat-production per kilogram of body-weight of the child is always notably higher than that of the adult.

Table 50.—*Heat-production per square meter of body-surface per 24 hours during fasts of 5 to 14 days*

Steer and dates of fasts	Days fasting													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	Hours without food													
	22–32	42–56	65–80	89–104	113–128	137–149	168–174	192–200	216–228	241–245	267–272	291–300	312–315	336–339
Steer C:	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*	*cal.*
Dec. 6 to 13, 1921	1,880	1,680	1,560	1,520	1,500	1,490	1,480	......	......	......	......	......	......	......
Jan. 4 14, 1922	1,960	1,890	1,690	1,500	1,600	1,510	1,520	1,400	1,510	1,590	......	......	......	......
Apr. 17 May 1, 1922	1,800	1,470	1,530	1,450	1,420	1,500	1,410	1,500	1,510	1,410	1,360	1,400	1,340	1,300
June 1 7, 1922	1,920	1,690	1,460	1,530	......	1,580	......	......	......	......	......	......	......	......
Nov. 6 16, 1922	[1] 2,090	[1] 1,780	[1] 1,690	[1] 1,520	[1] 1,550	......	......	1,590	1,680	......	......	......	......	......
Nov. 4 10, 1923	(2)	1,880	1,670	1,500	1,610	1,670	......	......	......	......	......	......	......	......
Mar. 3 13, 1924	1,290	1,110	1,180	1,220	1,230	1,200	1,270	1,240	1,230	1,150	......	......	......	......
Steer D:														
Dec. 6 to 13, 1921	2,080	1,680	1,690	1,620	1,600	1,550	1,530	......	......	......	......	......	......	......
Jan. 4 14, 1922	2,060	1,760	1,630	1,560	1,570	1,500	1,530	1,420	1,460	1,470	......	......	......	......
Apr. 17 May 1, 1922	1,740	1,630	1,560	1,440	1,430	1,410	1,410	1,420	1,410	1,360	1,460	1,390	1,390	1,400
June 1 6, 1922	2,130	1,830	1,810	1,620	1,740	......	......	......	......	......	......	......	......	......
Nov. 6 14, 1922	......	2,060	1,860	1,840	......	1,670	1,600	......	......	......	......	......	......	......
Nov. 4 9, 1923	2,490	2,090	1,830	1,790	1,650	......	......	......	......	......	......	......	......	......
Mar. 3 12, 1924	1,770	1,580	1,490	1,470	1,380	1,560	1,430	1,230	1,260	......	......	......	......	......
Steer E:														
Feb. 12 to 17, 1924	1,600	1,690	1,550	1,590	......	......	......	......	......	......	......	......	......	......
Steer F:														
Feb. 12 to 18, 1924	1,560	1,620	1,700	......	1,570	......	......	......	......	......	......	......	......	......

[1] Measurement made during period of lying and standing.

[2] A 24-hour heat-production of 2,480 calories per square meter of body-surface was noted when the steer had been 18 hours without food.

HEAT-PRODUCTION PER SQUARE METER OF BODY-SURFACE PER 24 HOURS

On pages 153 to 156 the calculation of the surface area of steers, based upon various formulas suggested by recent writers, has been discussed. It was there pointed out that Hogan's formula, in which the five-eighths power of the live weight in kilograms is multiplied by the constant 0.1081, probably gives a reasonably close measure of the true surface area in square meters. It is perhaps unfortunate that for the comparison of the same animal under different conditions of flesh during fasting, when striking differences take place within a relatively few days, a better means of determining the exact surface area is not available. In lieu of better surface-area measurements all of the calculations of the 24-hour heat-production per square meter of body-surface have been made employing this formula.[a] These calculations are summarized in Table 50 for the same fasts and animals as reported in Tables 48 and 49.

Exactly as with the total metabolism and the metabolism per 500 kg. of body-weight, there is a pronounced drop in the heat-production between the first and the second days of fasting per unit of body-surface and there is, in general, a still further drop as the fasts progress. The minimum value in the first six fasts again appears, in the case of steer C, on the fourteenth day of fasting, i. e., 1,300 calories. This value, however, is greater than that found on the first day of the fast in March 1924, following prolonged submaintenance feeding. The absolute minimum found with this animal is 1,110 calories on the second day of the March fast. With steer D the lowest value found prior to the fast in March 1924 was 1,360 calories on the tenth day of the April fast. On the eighth and ninth days of the fast following submaintenance feeding in March 1924, values of 1,230 and 1,260 calories, respectively, were noted, the first value being actually the lowest in the entire series with this animal.

In the case of steer C, in the fasts other than the last one, uniformity in the heat-production per square meter of body-surface appears at about the fourth day of the fasts, but the values for steer D do not approach uniformity until much later, i. e., on the seventh or eighth day. On the fifth day in the first six fasts of steer D there is an actual range in the values of from 1,430 to 1,740 calories, that is, 22 per cent. In view of the influence of undernutrition upon the fasting metabolism of both animals in March 1924, it is not surprising perhaps that these differences in metabolism are noted in the earlier fasts of these animals, which at times fasted after pasture feeding and at times after stall feeding with supposedly maintenance rations.

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[a] We wish to call attention here to the articles published recently by Brody and Elting regarding a new method proposed by them for measuring the surface area of cattle (Elting, Journ. Agric. Research, 1926, **33**, p. 269; Brody and Elting, Univ. Missouri, Agric. Expt. Sta., Bull. 89, 1926). These articles appeared after the manuscript of this monograph had been sent to the printer, and hence too late for us to make use of their body-surface formula in our calculations. Brody and Elting propose the equation $S = 0.15\ W^{0.56}$ as expressing the relation between body-weight and surface area, in which S equals the surface area in square meters and W the live weight in kilograms. At the moment of writing we are unconvinced that this is a real betterment of the Hogan formula, but if the new formula had been used for our steers, the body-surface values for steers C and D would be approximately 10 per cent lower than they are by Hogan's formula and those for steers E and F would be about 4 per cent lower. Hence, on this basis the values for the heat-production per square meter of body-surface would be 10 per cent and 4 per cent higher, respectively, than we have reported in this monograph.

A comparison of the values for the first day of the different fasts, excepting the fasts at the submaintenance level, shows no sign of uniformity between the two animals C and D. Steer D has a distinctly higher metabolic level than has steer C, the single exception being on the first day of the April fast, when his heat-production was a little lower than that of steer C. On the second day of fasting the values for the most part are higher with steer D than with steer C. This is also true in the case of the third day of fasting and, indeed, throughout essentially all of the succeeding fasting days, except that in the 10-day and 14-day fasts the metabolism of both animals is reasonably similar after the second day. In the fast following submaintenance feeding steer D is upon a definitely higher metabolic level than steer C until the eighth day is reached.

The values for the two smaller animals, E and F, on the basis of equal body-surface, are for the most part of the same order as those noted on the average with steers C and D, but they are notably higher than the values for steer C found in his fast after submaintenance feeding. The effect of submaintenance rations on steer D was much less pronounced for the first 7 days of fasting than it was with steer C. In this respect again, therefore, the evidence is that with steers E and F, which fasted at a submaintenance level, higher values for the metabolism per square meter of body-surface per 24 hours prevail than with one of the two adult animals, steer C, at a submaintenance level. Indeed, the values for steers E and F are a little higher than those for steer D at the submaintenance level, a fact which points again to the higher metabolism of the younger protoplasm.

Examination of all three bases for comparing the heat-production of these animals shows clearly that steer D is a distinctly different type from steer C, having a higher metabolism in all the fasts. This may be partly explained by the definitely greater stall activity of steer D, although our experience would lead us to believe that this difference in activity can not possibly account entirely for the difference in the metabolism of the two animals. Steers E and F, younger and lighter in weight, have a metabolism of an altogether different order from that of steers C and D. Their heat-production per square meter of body-surface more nearly corresponds to that of steer D than that of steer C, although it is somewhat higher than even that of the former. These comparisons bring out the influence of individuality in these animals. Indeed, the word "temperament" might be ascribed to the known restlessness of steer D. Experiments in which the nutritive plane is the same or essentially the same and in which the animals are lying quietly will be necessary to establish these differences quantitatively and sharply. That they exist is highly probable.

Heat-production in 2-day Fasts at a Maintenance Level of Nutrition

As is clearly brought out in Tables 48, 49, and 50 (pp. 173, 176 and 178), in which the data for the longer fasts are summarized, the most pronounced changes in metabolism due to fasting are to be observed in the first, second, and third days. Hence it seemed desirable to supplement the longer fasts by a series of short fasting experiments with steers C and D, in which emphasis would be laid upon the earlier stages of the fast. Furthermore, since it was evident that differences in nutritive level have a pronounced effect upon the fasting metabolism, these experiments were planned to rule out changes in nutritive level by having the animals fast in every case after an essentially maintenance ration. Opportunity was also taken to accentuate the influence of environmental temperature, in that many of the experiments were made under widely different temperature conditions. It is therefore impossible to compare directly the values obtained in these short fasting experiments with those obtained in the longer experiments, without taking into consideration the differences in environmental temperature and the fact that in the series of short fasts the animals were always studied at a maintenance level of nutrition, but that in the longer fasts they were studied after maintenance and submaintenance feeding and after coming from pasture. Furthermore, in comparing the first and second days of fasting in this series of 2-day fasts, it must be borne in mind that not infrequently the animals were arbitrarily subjected to marked changes in environmental temperature from one day to the next.

TABLE 51.—*Heat-production of steers C and D in 2-day fasts at a maintenance level of nutrition*

Steer and dates of fasts (1923)	Heat-production per 24 hours							
	Total				Per 500 kg.		Per sq. m.	
	Hours without food							
	25 to 26		47 to 50		25 to 26	47 to 50	25 to 26	47 to 50
Steer C:	*cal.*	° *C.*	*cal.*	° *C.*	*cal.*	*cal.*	*cal.*	*cal.*
Jan. 4 and 5[1]...	9,500	6.3	9,300	7.7	6,900	6,800	1,480	1,460
Jan. 22 and 23....	8,100	27.9	9,600	−1.9	5,900	7,000	1,260	1,500
Jan. 29 and 30....	11,200	2.9	6,800	24.9	8,100	4,900	1,740	1,060
Feb. 6 and 7....	9,600	2.6	10,400	2.0	6,900	7,500	1,490	1,610
Feb. 12 and 13....	9,800	3.9	9,600	1.7	7,100	7,000	1,520	1,500
Feb. 19 and 20....	10,700	2.5	11,900	−1.0	7,800	8,700	1,660	1,860
Mar. 2 and 3....	10,400	7.3	8,800	10.9	7,500	6,400	1,610	1,370
Mar. 9 and 10....	10,100	4.3	10,400	2.0	7,300	7,500	1,570	1,610
Mar. 16 and 17....	10,500	11.9	8,900	24.4	7,500	6,400	1,620	1,380
Mar. 23 and 24....	11,200	29.2	9,700	13.5	8,200	7,200	1,760	1,530
Average.......	10,100	....	9,500	....	7,300	6,900	1,570	1,490
Nov. 13, 1924......	....	....	11,900	24.4	....	7,800	....	1,740
Steer D:								
Jan. 10 and 11[1]...	11,300	7.0	10,200	7.0	8,200	7,400	1,760	1,590
Jan. 18 and 19....	11,100	3.4	8,300	28.2	8,000	6,000	1,730	1,290
Jan. 26 and 27....	11,900	8.8	7,600	28.3	8,600	5,500	1,850	1,190
Feb. 2 and 3....	10,300	27.9	9,200	7.3	7,600	6,800	1,610	1,450
Feb. 9 and 10....	11,300	8.6	10,200	5.7	8,200	7,500	1,760	1,600
Feb. 15 and 16....	12,000	−1.6	13,200	−7.5	8,600	9,600	1,860	2,050
Feb. 23 and 24....	11,400	3.6	11,600	0.2	8,200	8,400	1,770	1,810
Mar. 6 and 7....	11,400	2.1	11,600	0.3	8,300	8,400	1,770	1,810
Mar. 14 and 15....	11,200	10.5	10,700	22.8	8,100	7,700	1,730	1,660
Mar. 21 and 22....	11,600	12.6	10,400	29.0	8,400	7,600	1,800	1,620
Average.......	11,400	....	10,300	....	8,200	7,500	1,760	1,610

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[1] On Jan. 6 and 12, with steers C and D, respectively, the 24-hour heat-production 72 hours after food was as follows: Steer C, 8,800 cal. per 24 hrs.; 6,500 cal. per 500 kg.; 1,380 cal. per sq. m.; steer D, 8,900 cal. per 24 hrs.; 6,500 cal. per 500 kg.; 1,390 cal. per sq. m.

The values for the computed heat-production during this series of 2-day fasts are summarized in Table 51, being reported on the three different bases of the total 24-hour heat-production, the heat-production per 500 kg. of body-weight per 24 hours, and the heat-production per square meter of body-surface per 24 hours. In addition, the average chamber temperature prevailing on each day when the metabolism was measured is given at the right of the values for the total 24-hour heat-production.

A comparison of the values for the total 24-hour heat-production is justifiable, since in the short period of 3 months during which the animals were studied, their body-weights did not alter materially, because they were always upon a maintenance level of nutrition. On the first day of fasting, i. e., 25 to 26 hours after food, the total heat-production of steer C ranged from 8,100 calories on January 22 to 11,200 calories on January 29 and March 23. With steer D the metabolic level was higher, the lowest value being 10,300 calories on February 2 and the highest being 12,000 calories on February 15. Contrary to our usual custom with these animals in the longer fasts, the 2-day fasts were not made under the same temperature conditions and on the same dates with each animal. Disregarding for the moment the differences in environmental temperature, we find that the average 24-hour heat-production of steer C on the first day is 10,100 calories and of steer D 11,400 calories. Since these animals were of almost the same weight, the metabolism of steer D on this basis is about 13 per cent higher than that of steer C. The average chamber temperature during the experiments with steer C was 9.9° C. and with steer D 8.3° C., i. e., somewhat lower. Hence it might be argued that the higher metabolism noted with steer D might be accounted for by the fact that the average environmental temperature was lower in his case. A close examination of the figures on individual days shows that the minimum metabolism of steer C, 8,100 calories, occurred on January 22, when the environmental temperature was 27.9° C. On the other hand, the maximum metabolism, 11,200 calories, occurred on January 29 with an environmental temperature of 2.9° C., and also on March 23 with an environmental temperature of 29.2° C. Hence with steer C the effect of the temperature is not clear-cut. With steer D the lowest value, 10,300 calories, is found on the day with the highest temperature, 27.9° C., and the highest value, 12,000 calories, is found on the day with the lowest temperature, –1.6° C. The difference between these two heat values represents an increase in metabolism of 16.5 per cent with a fall in temperature of approximately 30°. Although extremely high temperatures did not prevail on any of the other experimental days, an examination of the data for the individual days other than these two days shows that it is difficult to find a distinct trend of low metabolism on days with the higher temperatures and high metabolism on days with the lower temperatures. Indeed, the general picture for the two animals together does not indicate a definite effect of temperature.

On the second day of fasting, 47 to 50 hours after the last food, lower values as a rule obtain with both animals, as is to be expected from the analysis of the data for the long fasts. With steer C the lowest value on the second day is 6,800 calories with a temperature of 24.9° C., and the highest value is 11,900 calories with a temperature of –1.0° C. Here there is seemingly clear evidence of an effect of environmental temperature, and yet an examination of the values on other dates shows that although in general the metabolism is higher the lower the temperature, this is by no means invariably the case. With steer D the lowest metabolism on the second day is 7,600 calories on January 27 with a temperature of 28.3° C., and the highest is 13,200 calories on February 16 with a temperature of −7.5° C. Here again a higher metabolism is noted with a low temperature, and yet with the high temperature on March 22 the metabolism is 10,400 calories as compared with 7,600 calories on January 27, when the temperature was also high.

The influence of temperature may furthermore be specially studied by comparing the instances where great differences in temperature were artificially produced on two consecutive days. Thus, with steer C on January 22 the temperature was held at 27.9° C., and the next day at −1.9° C. In spite of the fact that in the experiment made at −1.9° C. steer C had been fasting for 2 days, the 24-hour heat-production was 9,600 calories as compared with 8,100 calories on the first day at 27.9° C. In the next fast, on January 29 and 30, the increase in temperature on the second day has accentuated the normal fall in metabolism on the second day of fasting, since on the first day the metabolism was 11,200 calories at 2.9° C. and on the second day at 24.9° C. it was but a little over one-half as great, i. e., 6,800 calories. On February 19 and 20 the metabolism was a little higher on the second day than on the first, but apparently with the low temperatures, such as prevailed on March 9 and 10, the influence of fasting is less pronounced, for with essentially the same temperature on both days the metabolism is the same. On January 18 and 19, with steer D the increase in temperature on the second day accentuated the normal loss in heat-production as a result of fasting. This is also true on January 26 and 27. On February 15 and 16 a drop in temperature of 6° has seemingly raised the metabolism on the second day actually above that on the first, and yet on March 15 a rise of 12° in the temperature hardly influenced the heat-production. On November 13, 1924, at a temperature of 24.4° C., steer C produced 11,900 calories on the second day, a value which is identical with the highest value on the second day noted on February 20, 1923, and yet on November 13, 1924, the environmental temperature was 24.4° C. while on February 20, 1923, it was −1.0° C.

An examination of the records of stall temperature during the 24 hours immediately preceding the metabolism measurements during these short fasts indicates that in nearly every instance the stall temperature was essentially the same as the chamber temperature during the respiration experiment. There were a few cases, however, when the stall temperature was markedly different from the chamber temperature. Thus, on March 17, 1923, steer C was placed in the respiration chamber at a temperature of 24.4° C., after having been for 24 hours previous in his stall at a temperature of 8° C. On March 24, 1923, the chamber temperature was 13.5° C. as compared with a stall temperature of 22° C. during the preceding 24 hours. Similarly, in the case of steer D on March 15, 1923, the stall temperature had been 5° C. and the chamber temperature was 22.8° C., and on March 21, 1923, the stall temperature had been 24° C. and the chamber temperature was 12.6° C. It is possible that a sudden marked change in temperature may cause a temporary disturbance in the animal's heat-loss and heat-production. Experiments made under such conditions do not, therefore, lend themselves to the study of the effect of a high or low environmental temperature upon metabolism so well as do experiments made under conditions when the animal has been living for one or two weeks at least at the same environmental temperature in the stall as is to prevail during the respiration experiment. It was therefore planned to include in our research a series of experiments made under such conditions, to study the effect of wide differences in temperature. These experiments will be considered later (see pp. 200 to 202).

On January 6 and 12, respectively, the metabolism of steers C and D was studied 72 hours after food and was found to have fallen perceptibly in both cases, with no very pronounced changes in the environmental temperature. This finding is in line with the picture shown in the longer fasts.

It is hardly feasible to compare the metabolism on the first and second days of the short fasts (see Table 51, p. 181), with the metabolism on the same days in the longer fasts (see Table 48, p. 173), for there were differences in body-weights in the longer experiments, and no averaging of the data in Table 48 is justifiable on account of the different metabolic levels at which the longer fasts began.

A further factor which prevents a comparison of the short fasts with the longer fasts is the influence upon metabolism of the marked temperature differences designedly employed in the series of short fasts. It is only when the metabolism is computed upon the basis of equal size, that is, per 500 kg. of body-weight or per square meter of body-surface, that any comparisons are justifiable. But even on this basis one must carefully avoid comparison with the experiment in March 1924, which was made at a submaintenance level, and one must also bear in mind the influence of sudden changes in environmental temperature.

The picture of the 24-hour heat-production per 500 kg. of body-weight during the 2-day fasts in 1923 is essentially the same as that of the total heat-production, for the body-weights of the two animals were essentially alike and changed but little throughout the series of fasts. Much the same picture is also shown by the heat-production per square meter of body-surface. An extraordinarily low value of 1,060 calories per square meter of body-surface was noted with steer C on January 30 with an environmental temperature of 24.9° C. and a low value of 1,190 calories was noted with steer D on January 27 with an environmental temperature of 28.3° C. These two figures more nearly approximate the conventional 1,000 calories per square meter of body-surface, which many physiologists believe represents the general heat-production of warm-blooded animals. Too little is as yet known, however, with regard to the influence of environmental temperature upon animals to make any generalizations. It is hardly conceivable that the normal environmental temperature of a ruminant should be 25° to 28° C. or higher, and yet this temperature more nearly approximates the "private climate"[a] of the clothed human than does the ordinary stall

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[a] Dorno, C., Medical climatology and high-altitude climate, Vieweg and Son, Brunswick, 1924, p. 58.

temperature or, indeed, the conventional 20° C. maintained in the ordinary experiments in the respiration chamber or respiration calorimeter. If these low values had been repeatedly found, much more credence could be given to their significance. They do not appear in the long fasts, where one would expect, if anywhere, to find a very low heat-production per square meter of body-surface. Indeed, the lowest values noted in the long fasts, other than in the fasts following submaintenance feeding, were 1,300 calories per square meter of body-surface with steer C and 1,360 calories with steer D. All of these measurements, however, were made with the animal standing, and it may be argued that the difference above the conventional 1,000 calories per square meter of body-surface may be in large part explained by the extra effort of standing. Further discussion of this point will be deferred until later (see p. 218). It is sufficient to state at this point that it is not believed that the difference in metabolism in the two positions can possibly explain the values noted for the heat-production per square meter of body-surface.

Measurement of Fasting Metabolism in Three Consecutive 24-hour Periods

The basic principle of studying the metabolism of ruminants in short periods has frequently been challenged. The history of the change from long to short periods in the study of the metabolism of ruminants is not unlike that with other animals and humans. Practically all of the work on humans by Atwater and his associates with the respiration calorimeter at Wesleyan University, Middletown, Connecticut, was based upon 24-hour periods. Armsby, building a calorimeter on the model of the Wesleyan University apparatus, likewise used the 24-hour period. With humans it was soon seen that much valuable information could be obtained at far less expense by making metabolism measurements in shorter periods, from which the probable 24-hour metabolism could be computed. The 24-hour period, which includes the profound influence upon metabolism of variations in muscular activity, body position, and digestion of food, is a near composite of the daily life, but a period of this length gives no true knowledge with regard to the basal metabolism, the increment due to change in position, or the increment due to food. All of these features must be determined in short periods.

It was recognized at the outset that it would be impossible to attempt to prescribe any definite, predetermined degree of muscular activity or repose in the case of these non-cooperating ruminants. The peak effect of the digestion of food was avoided in the short periods of measurement by studying the animal 24 hours after the ingestion of food, and variation in body position was avoided by making it impossible for the animal to lie down, although the activity during standing was not controllable and therefore variable. The animals were prevented from lying down primarily because it was assumed that there is a difference of from about 10 to 30 per cent in the metabolism of an animal in the standing as compared to the lying position. It was impossible to make the animal lie down and remain lying the entire time, but he could be kept standing up. Under these conditions the so-called "standard metabolism" measurements were made. Are measurements of the metabolism under such conditions suitable for pre-

TABLE 52.—*Metabolism of fasting steers, measured in three consecutive 24-hour periods*

Steer, date, live weight, and average chamber temperature (1924)	Hours standing	Hours lying	Hours without food to beginning of experiment	Carbon dioxide produced in 8 hours	Respiratory quotient	Heat produced per 24 hours		
						Total	Per 500 kg.	Per sq. m.
Steer F:				*gm.*		*cal.*	*cal.*	*cal.*
Apr. 1......	4½	3½	24	881.6	0.84	7,800	13,200	2,060
295.2 kg...	3½	4½	32	844.8	(.80)	7,700	13,000	2,040
11.6° C...	1½	6½	40	744.0	(.78)	7,000	11,900	1,850
Average	9½	14½	....	823.5	....	7,500	12,700	1,980
Apr. 2......	4	4	48	750.4	(.76)	7,200	12,700	1,960
(283.0 kg.)	6	2	56	737.6	(.74)	7,200	12,700	1,960
16.3° C...	2	6	64	700.8	(.73)	6,900	12,200	1,880
Average...	12	12	....	729.6	....	7,100	12,500	1,930
Apr. 3.......	5	3	72	705.6	(.71)	7,100	13,100	1,970
271.8 kg...	5	3	80	699.2	(.71)	7,100	13,100	1,970
18.0° C...	2	6	88	689.6	.71	7,000	12,900	1,940
Average.....	12	12	....	698.1	....	7,100	13,000	1,960
Steer E								
Apr. 9....	6	2	24	886.3	.82	8,000	14,300	2,190
280.0 kg...	6	2	32	786.9	(.80)	7,200	12,900	1,970
17.7° C...	6	2	40	810.2	(.78)	7,600	13,600	2,080
Average.....	18	6	....	827.8	....	7,600	13,600	2,080
Apr. 10.....	7	1	48	728.8	(.76)	7,000	13,000	1,960
(270.0 kg.)	3	5	56	728.1	(.74)	7,100	13,100	1,980
17.4° C....	3	5	64	736.5	(.73)	7,300	13,500	2,040
Average.....	13	11	....	731.1	....	7,100	13,200	1,990
Apr. 11.....	5	3	72	763.7	(.71)	7,700	14,800	2,200
260.8 kg...	8	0	85	[1]713.6	.71	[1]7,200	[1]13,800	[1]2,060
18.0° C....	3	5	88	659.7	.71	6,700	12,800	1,890
Average...	16	8	....	712.3	....	7,200	13,800	2,050
Steer C:								
Apr. 23.....	5	3	24	1,317.2	.89	11,100	8,300	1,760
669.6 kg...	3	5	32	1,171.0	(.80)	10,700	8,000	1,700
19.6° C....	3	5	40	1,167.1	(.78)	10,900	8,100	1,730
Average.....	11	13	....	1,218.4	....	10,900	8,100	1,730
Apr. 24.....	5	3	48	1,145.5	(.76)	10,900	8,500	1,770
(644.8 kg.)	4	4	56	1,035.9	(.74)	10,100	7,800	1,640
20.7° C....	4	4	64	991.6	(.73)	9,800	7,600	1,590
Average.....	13	11	....	1,057.7	....	10,300	8,000	1,670
Apr. 25.....	6	2	72	997.9	(.71)	10,100	8,100	1,680
620.0 kg...	4	4	80	963.5	(.71)	9,700	7,800	1,610
17.4° C....	4	4	88	944.6	.71	9,500	7,700	1,580
Average.....	14	10	....	968.7	....	9,800	7,900	1,620

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[1] Based on a period of 2 hours and 58 minutes, because electric power went off at start of 8-hour period.

TABLE 52.—*Metabolism of fasting steers, measured in three consecutive 24-hour periods*—Cont.

Steer, date, live weight, and average chamber temperature (1924)	Hours standing	Hours lying	Hours without food to beginning of experiment	Carbon dioxide produced in 8 hours	Respiratory quotient	Heat produced per 24 hours		
						Total	Per 500 kg.	Per sq. m.
Steer D:				*gm.*		*cal.*	*cal.*	*cal.*
May 14.....	8	0	24	1,499.7	0.92	12,300	9,300	1,960
664.6 kg...	6	2	32	1,437.0	(.80)	13,200	9,900	2,100
24.4° C....	5	3	40	1,246.1	(.78)	11,700	8,800	1,860
Average.....	19	5	....	1,394.3	....	12,400	9,300	1,970
May 15.....	5	3	48	1,264.9	(.76)	12,100	9,400	1,970
(643.0 kg.)	4	4	56	1,256.0	(.74)	12,300	9,600	2,000
24.4° C....	3½	4½	64	1,133.6	(.73)	11,200	8,700	1,820
Average.....	12½	11½	....	1,218.2	....	11,900	9,200	1,930
May 16	5	3	72	1,170.8	(.72)	11,700	9,400	1,940
621.4 kg...	4	4	80	1,129.8	(.72)	11,300	9,100	1,880
22.4° C....	4	4	88	1,128.6	.72	11,300	9,100	1,880
Average.....	13	11	....	1,143.1	....	11,400	9,200	1,900

dicting the 24-hour metabolism of a stall-confined animal? Are they suitable for computing the basal or the lowest metabolism of an animal, or do they have the same error involved in the 24-hour experiments with men, in that the variable activity makes computations of any fundamental values highly unsatisfactory?

In the discussion of the 2-day fasts (see p. 184) it was pointed out that the 24-hour heat-production per square meter of body-surface was invariably higher and generally much higher than the conventional 1,000 calories commonly ascribed to all warm-blooded animals. It was suggested that this might be due to the environmental temperature and to the fact that our animals were standing instead of lying. To rule out the error in the computation of the 24-hour metabolism from a 2-hour period of measurement, it was decided to make some experiments with the animal fasting inside the respiration chamber, to begin the experiment 24 hours after the last food was eaten, and to continue it for three consecutive 24-hour periods. The animal was to be allowed to lie or stand at will. No food was given, but drinking-water was supplied. The length of time that the animal stood and lay down was carefully recorded. The usual kymograph records of the activity of the animal in the chamber stall were kept, although the records were at times vitiated by defects in the tambour, so that they do not serve the purpose of exactly quantitating the degree of activity in all cases. The temperature element was ruled out, in that essentially the same temperature was maintained on each day in any given experiment with an animal. In the different experiments with the different animals there were, however, small differences in temperature (see p. 189). Four such experiments were made in April and May 1924, one with each of the four steers. The results are tabulated in Table 52.

Prior to these experiments, a 24-hour respiration experiment had been made with steer C, primarily to test the feasibility of making 24-hour experiments with this apparatus and with our undermanned staff. A technique was finally devised whereby 24-hour experiments could be carried out and the carbon-dioxide production collected in 8-hour periods. It was impossible to secure duplicate aliquots of the chamber air during these 8-hour periods, and each carbon-dioxide measurement therefore depends upon the increment in weight of one set of absorbing bottles, which were connected with and disconnected from the ventilating system at the beginning and end of each period. Utmost precautions were taken to check not only the actual weights on the pan, but to check the oscillation of the balance and to check the absence of gaskets used to connect the bottles with each other. Every precaution was therefore taken to avoid errors in weight. But the determinations were not made in duplicate, and hence are remotely liable to possible error. From a subsequent examination of the data, however, we feel confident that rarely can the presence of an error be suspected. As pointed out in an earlier discussion of the technique used with this apparatus,[a] after several months' experience with a double system of absorbers in which duplicate quantities of air were collected, the agreement between duplicate samples was almost without exception of the highest order, particularly after the first few months of experimentation. This agreement in duplication was so exact that we felt justified in reducing the number of absorbing trains to one for each period, thereby making it possible for our small staff to carry out these long experiments. Originally it was planned to use the apparatus only for a series of perhaps four half-hour periods, in which to a certain extent each half-hour period would be a check upon the other periods. Although duplicate measurements were not possible in the 8-hour periods, each subsequent 8-hour period may be looked upon as a check upon the one prior to or following it, particularly when the animal is fasting. In the transitional period from feeding to fasting such can not, of course, be the case. On the whole, however, the possibility of error is remote, but we feel it our duty to call attention to it.

The carbon-dioxide measurements reported in Table 52 were all made in 8-hour periods, save in the second period on April 11 with steer E, when, owing to an unavoidable interruption in electric power, it was possible to secure a measurement only for 2 hours and 58 minutes. In this case, however, an analysis of the carbon-dioxide residual in the chamber was made at the beginning and end of the period so as to make it possible to compute the 8-hour carbon-dioxide production from the measurement for 2 hours and 58 minutes. Although the discussion of these experiments will be based for the greater part upon the computations on the 24-hour basis, the carbon-dioxide measurements are reported on the 8-hour basis because they were actually determined in this length of time and will serve to show the trend of the fasting metabolism, particularly on the first day.

The respiratory quotient was determined at the beginning of the first 8-hour period of the three days and again at the end of the fast. For the computation of the heat values in the intervening periods when the respira-

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 67.

tory quotient was not actually determined, assumptions have been made, based upon an extensive series of actual determinations with animals under conditions closely approximating those obtaining in these experiments. The rate of fall in the respiratory quotient is obviously most rapid on the first day, but on the third day the quotient was found to be almost uniformly a fasting quotient of 0.71 or 0.72. It would have been preferable to have determined the respiratory quotient in each period, but this was impossible with the small staff at our disposal. It is hardly probable, however, that any serious error has been introduced by the interpolated quotients given in Table 52.

The heat-production during each 8-hour period is recorded on the usual three bases of the total 24-hour heat-production, and the 24-hour heat-production per 500 kg. of body-weight and per square meter of body-surface. Although it would seem as if this calculation should be made upon the 8-hour basis, for purposes of comparison with the computed metabolism in other experiments it seems best to make the calculations on the 24-hour basis. The average heat-production for the day, however, has the greatest value.

It is unfortunate that the chamber temperature could not have been the same in the case of all four animals. On the first day of the first experiment, unexpectedly cold weather and a fall of snow made such heavy demands upon our heating system that the temperature could not be maintained above an average value of 11.6° C. On the other hand, in the middle of May, the warm environmental temperature made it impossible to carry out the experiment with steer D at a temperature below about 24° C., which prevailed for the 3 days.

For several weeks prior to these 3-day experiments the steers had been receiving supposedly maintenance rations, but they had probably in no case sufficiently recovered from the preceding period of submaintenance feeding, followed by fasting, and the nutritive state was undoubtedly somewhat below par. Steers C and D had fasted for 10 and 9 days, respectively, following 10 weeks on a submaintenance ration, and then each was given 9 kg. of hay daily, a supposedly maintenance ration. Steer C was subjected to a 4-day fast beginning on April 22, after having been only 39 days on the ration of 9 kg. of hay to recover from the stringent ration reduction and the 10-day fast. Steer D did not commence his 4-day fast until three weeks later, so that he had a better opportunity for complete recuperation. Steers E and F had likewise been subjected to a long period of submaintenance feeding lasting 8 weeks, followed by a 5-day and a 6-day fast, respectively, and then they were given a maintenance ration of 5 kg. of hay and 0.91 kg. of meal daily for 4 or 5 weeks prior to the continuous 3-day metabolism measurements. At this time they were distinctly underweight, for although they weighed the same as they had 6 months before, when they were first received at the laboratory, they should normally have weighed much more, since they were young, growing animals. All four steers were therefore under-nourished rather than over-nourished at the time of these experiments, and from the well-known influence of undernutrition upon metabolism, one could expect that these animals would have a low rather than a high metabolism, and hence that the values found with them would be minimum rather than maximum. It will be seen later (see p. 191) that the metabolism per square meter of body-surface was as high in these experiments as in the earlier fasts at the maintenance level of nutrition, and we have reason to believe that if the level of nutrition at the time of these experiments in 1924 had been a full maintenance one, the measured metabolism would have been even higher than it was found to be.

All four experiments began and ended between $7^h 30^m$ a. m and 8 a. m. Each animal was inside the respiration chamber for 72 consecutive hours, the first period beginning 24 hours after the last ingestion of food. (See Table 11, p. 53, for record of last feed prior to the experiment.) The body-weights were determined at the beginning and end of each experiment, but the weight for the second day had to be assumed, based upon the average of the initial and final weights. Steer C drank no water during his experiment. Steer D drank 14 kg. The amount taken by steers E and F is unknown.

An examination of the data in Table 52 for the hours spent in standing and lying indicates that in the first experiment steer F spent in general about half the day standing and half the day lying, although the lying period on the first day was a little longer than the standing period. Sometimes the lying period in any 8-hour period might be extended to 6 hours or reduced to 1 or 2 hours, or the animal might stand the entire 8 hours. In the fasts of 5 to 14 days the animals were inclined to spend from 14 to 15 hours each day lying down. In these continuous 3-day experiments, on the contrary, the animals generally stood each day at least 50 per cent of the time, for only on the first day of the fasts with steer F and with steer C was the time spent in lying greater than the time spent in standing. The kymograph records of activity are complicated by the fact that occasionally the apparatus was defective. From an inspection of these records for the 3-day experiments in 1924, it would appear that steer D was somewhat more restless than steer C, and steer E was more restless than steer F. A general inspection of the kymograph records for all the experiments throughout the whole period of research also indicates that steer D was more restless than steer C, but that there was little difference between the activities of steers C, E, and F. It is believed that steer D was, on the whole, a little more restive than any of the other three animals, although in general all of the animals were remarkably quiet inside the chamber. Our experience with our first group of 12 steers in the research on undernutrition showed the degree of restlessness which can be expected inside the respiration chamber from an untrained animal. Judged on the basis of this experience, steers C, D, E, and F were highly trained and remained extraordinarily quiet even for stall-confined animals.

The carbon-dioxide production usually falls off markedly in the successive periods on the first day, and the decrease continues on the next two days. The minimum value in every case occurs in the last period of the experiment, indicating that the lowest carbon-dioxide production had not been obtained at that time, a finding fully in conformity with the persistent decrease in metabolism noted in the fasts of 5 to 14 days.

There is likewise usually a distinct decrease in the computed 24-hour heat-production on the three successive days of each fast. Steers E and F have a much lower heat-production than steers C and D. Thus, on the first day of the fast the older steers had an average 24-hour heat-production of about 11,600 calories, and the younger steers of about 7,550 calories. This is instantly explainable by the large differences in body-weight, for the young steers actually weighed less than half of what the older steers weighed. Hence we are quite prepared to find that the heat-production of steers E and F per 500 kg. of body-weight reflects strikingly the influence of the younger protoplasm.

On the basis of uniformity in weight a decrease in the heat-production still appears, although it so happens that with both steers E and F the maximum heat-production per 500 kg. of body-weight is on the third day. On the whole, however, the differences are not striking, and one is not justified in saying that the heat-production per 500 kg. of body-weight undergoes any special alteration in the course of a 3-day fast beginning 24 hours after the withholding of food. This being the case, it is not surprising that the heat-production per square meter of body-surface usually remains uniform during the fast. Steer D has a larger heat-production than steer C on this basis, as on the other two bases, perhaps accounted for by his distinctly greater activity. Steer C has a measurably lower heat-production per square meter of body-surface than the younger animals, E and F, but steer D has essentially the same heat-production per square meter of body-surface as does steer F, a fact which might be cited as excellent evidence in favor of the idea of uniformity in heat-production per square meter of body-surface. Since the metabolism of steer D was influenced by greater muscular activity than was the case with steers E, F, and C, the metabolism of steer C should more properly be compared, perhaps, with that of steers E and F. Such comparison shows that steer C has a much lower heat-production per square meter of body-surface than either steer E or steer F. The average heat-production of the two younger animals, on this basis, is not far from 2,000 calories, as compared with an average value of 1,670 calories in the case of steer C. In other words, the younger animals have a metabolism essentially 20 per cent higher than that of steer C.

These fasting values may be compared with those noted in Table 50 for the heat-production per square meter of body-surface per 24 hours in the period from 42 to 56 hours after the last food, naturally disregarding the values for the fast in March 1924. The average heat-production of steer C at this period of fasting in the longer fasts was 1,730 calories per square meter of body-surface, i. e., essentially the same as the average value of 1,670 calories found in the 3-day experiment in April 1924. Similarly the somewhat higher values noted with steer D in Table 52 are confirmed by the data in Table 50 for the long fasts. The measurements on the first day of the long fasts were made 22 to 32 hours after food, and those on the first day of the fast in May 1924 were made 24 to 40 hours after food, so that the time interval after food ingestion is essentially the same in both cases. The average value noted for steer D in the long fasts, omitting that in March 1924, is 2,100 calories as compared with 1,970 calories on May

14, 1924. For the second day the average value in the long fasts is slightly below 1,800 calories as compared with 1,930 calories on the second day of the 1924 experiment. On the third day three values in the long fasts are around 1,800 calories, the remainder being all perceptibly below 1,800 calories, as compared with 1,900 calories on the third day of the fast in May 1924.

These comparisons justify the conclusion that the short experiment of four half-hour periods, even with the animal standing the entire time, gives a computed heat-production which is not far from that found in 24-hour periods when the animal is allowed to stand or lie at will. From the criticisms raised against the short period, one would infer that the values computed from short periods would in general be higher than those found in long periods. This is not the case in the comparisons just made. It is true that on the first two days of the fast of steer C in April 1924 values slightly lower than the average values on the first two days of the long fasts are recorded, but in the fast in April 1924 steer C was an undernourished animal, having had but 5 weeks to recover from a 10-day fast which followed a long period of submaintenance. The heat-production of steers E and F on the several bases of computation was higher in the continuous 3-day experiments than in the fasting experiments of February 1924, following submaintenance feeding. Unfortunately, no fasting experiments were made with steers E and F following maintenance feeding, on the basis of four half-hour periods of measurement.

So far as the evidence goes, it points toward the legality of computing the fasting metabolism from four half-hour periods of measurement. Indeed, the justification for the use of the half-hour period is far greater in the case of fasting experiments than it would be in the case of experiments when the animals receive food regularly, for in the transitional stage following the digestion of food the peak of digestive activity occurs at different periods, depending upon the nature and the amount of food ingested. We have not studied food problems in experiments of four half-hour periods, but we have used the short half-hour periods in studying the influence of the ingestion of food, that is, the rapidity of digestive activity and the increment in metabolism due to such activity. These experiments will be considered subsequently (see p. 222).

Comparison of the Metabolism During 2 Days on Food, Followed by 2 Days Without Food, at Maintenance and Submaintenance Levels and at High and Low Environmental Temperatures

The state of nutrition has not been seriously considered, at least in the case of humans, as affecting the fasting metabolism, but our experience with steers in the series of long and short fasts indicated that the nutritive level at which the fast begins has a great influence upon the fasting metabolism. To study specifically the influence of different feed-levels, therefore, a series of 4-day respiration experiments were made with steers E and F in 1925. The animals were confined in the respiration chamber as they would be in a stall in the barn, and were allowed to stand and lie at will. During the first two days they received feed and drinking-water as usual. During the last two days no feed was given, but water was offered as usual. In some experiments a maintenance ration of hay was given on the 2 feed days and in others a submaintenance ration, the animals having been upon the particular feed-level under consideration for at least 2 weeks prior to the respiration experiment. The ration was, furthermore, altered not only with regard to the quantity of metabolizable energy, but also qualitatively with regard to the character of the feed, timothy hay being fed in some experiments and alfalfa hay in others. The selection of the timothy and alfalfa hay, however, was not made for the purpose of considering the relative merits of these two feedstuffs for maintenance or for preparing the animal to resist a fast, but because these two substances are by common consent considered typically different in character, and it was desired, if possible, to alter considerably the character as well as the quantity of the ration.

The effect of extreme variations in environmental temperature was also introduced in this series of 4-day experiments. In the earlier series of short fasts the influence of environmental temperature had been studied, but it was believed that in that series the picture of the effect of the environmental temperature reflected only the first reaction of the animal to a sudden change in temperature. Hence, in the 1925 series the animal was purposely kept for approximately two weeks in a stall temperature essentially the same as that which was to be maintained in the respiration chamber during the 4-day experiment. Environmental temperatures varying from 23.3° C. to as low as 3.6° C. were accordingly studied. So far as the comparison of timothy and alfalfa hay is concerned, the data are reasonably complete for both steers. Uncontrollable conditions with regard to the temperature, however, made it impossible at times to secure as low a temperature and as satisfactory uniformity in temperature control as was wished. The data in this respect, therefore, are not complete for steer F, but are fortunately more complete for steer E both at the maintenance and submaintenance levels of nutrition.

The influence of a maintenance and submaintenance level of nutrition and of two different feedstuffs upon the metabolism both during feeding and fasting was thus determined. Furthermore, the plan of the experiments made it possible to secure evidence as to the accuracy of the method of computing the fasting katabolism from the measured metabolism of the animal when upon two different feed-levels. Indeed, one of the main objects of the experiments was to obtain information on this point. Other evidence was furnished by this series of experiments regarding the influence of the nutritive level, the character of the feed, and the environmental temperature upon the metabolism during the transitional stage on the first day of fasting. It was believed that the profound effect of the submaintenance ration upon the level of the fasting metabolism would be reflected somewhat in the metabolism when the animal was receiving submaintenance rations, and particularly in the transitional stage on the first day of fasting. Indeed, the measurement of the metabolism during this transitional period would serve to indicate the value of the different types of feed and of the two different nutritive levels in enabling the animal to withstand the fast, inasmuch as it would give an idea as to the rapidity and intensity of the drafts upon the body compounds. In addition, the determination of the actual level to which the metabolism falls during two days of fasting should furnish an excellent control upon the earlier measurements made in short half-hour periods and, indeed, should compare reasonably well with the level noted in the continuous 3-day fasting experiments made in the spring of 1924.

The data secured with steers E and F during this series of 4-day experiments are summarized in Table 53. Each day began at $4^h 30^m$ p. m. The carbon-dioxide production was determined quantitatively in two 8-hour periods and two 4-hour periods each day. The residual air inside the respiration chamber was analyzed at the end of each period, and the respiratory quotient was determined for nearly every period. The data are therefore available for computing the heat-production during each of the 8-hour periods as well as during the entire 24-hour periods. Space does not permit the printing of all the 8-hour values, unfortunately, and in Table 53 only the 24-hour values have been recorded. It is believed, however, that the picture of the metabolism under the special conditions studied will be best illustrated by these 24-hour values, since the difficulty of working with a non-cooperating ruminant makes the use of the 8-hour period, particularly during feed days and in the transitional stage from feeding to fasting, of questionable value. If it were possible to rule out muscular activity while studying the metabolism during the first 48 hours after the withholding of food, then a 4-hour or 8-hour period of measurement would be of great importance.

In accordance with the method of calculation employed in presenting the energy values in the earlier fasts, the heat-production during these 4-day experiments has been computed from the carbon-dioxide production and the respiratory quotient in all cases where the respiratory quotient was 1.00 or below, and from the computed oxygen consumption and the calorific value of oxygen at a quotient of 1.00 in those cases where the respiratory quotient was above 1.00. (See pp. 147 to 150.) The heat values are reported on the three bases of the total heat-production per 24 hours and the 24-hour heat-production per 500 kg. of body-weight and per square meter of body-surface.

It was impossible to weigh the animal except at the beginning and end of these experiments. Hence the body-weights on the intermediate days are interpolated, on the assumption that during the first two days with feed the body-weight would remain unchanged and that on the first fasting day there would be a decrease equivalent to the amount of the daily ration withheld. The body-weight reported in Table 53 for the first day of each experiment is not, however, the weight on that particular day, but is an average weight based upon the weight on that day and on 6 days preceding. The urine voided was collected each day with but few exceptions. The feces could not be collected daily and were allowed to accumulate in a large, air-tight container underneath the respiration chamber (see Fig. 2, p. 26).

In the belief that there would be a distinct difference in the general physical activity of the animal on days with feed and days without feed, kymograph records of the degree of activity were kept and an approximate

Table 53.—*Summary of 4-day respiration experiments with steers E and F*

Steer and date[1] (1924–25)	Live weight	Hours standing	Hours lying	Hay eaten in 24 hours[2]	Hours without food to beginning of day	Average stall temperature week before experiment	Average chamber temperature	Heat produced per 24 hours		
								Total	Per 500 kg.	Per sq. m.
Steer E:	*kg.*			*kg.*		*°C.*	*°C.*	*cal.*	*cal.*	*cal.*
Dec. 12–13	368.8	14	10	7.0	0	24	22.5	11,800	16,000	2,720
Dec. 13–14	(368.8)	11	13	7.0	0	....	22.5	11,500	15,600	2,650
Dec. 14–15	(361.8)	9½	14½	0.0	8	....	22.2	8,900	12,300	2,070
Dec. 15–16	349.4	7½	16½	0.0	32	....	22.1	7,700	11,000	1,830
Jan. 13–14	351.4	13	11	3.5	0	25	22.3	8,200	11,700	1,940
Jan. 14–15	(351.4)	10½	13½	3.5	0	....	22.7	7,900	11,200	1,870
Jan. 15–16	(348.0)	10½	13½	0.0	24	....	22.6	6,800	9,800	1,620
Jan. 16–17	333.4	12½	11½	0.0	48	....	22.6	6,000	9,000	1,470
Feb. 2– 3	337.6	17½	6½	3.5	0	4	4.7	9,000	13,300	2,190
Feb. 3– 4	(337.6)	11	13	3.5	0	....	5.1	9,200	13,600	2,240
Feb. 4– 5	(333.8)	17	7	0.0	24	....	5.7	7,200	10,800	1,760
Feb. 5– 6	322.8	11½	12½	0.0	48	....	8.8	6,500	10,100	1,630
Feb. 27–28	359.0	10½	13½	7.0	0	11	3.6	11,000	15,300	2,580
Feb. 28–Mar. 1	(359.0)	9	15	7.0	0	....	6.1	11,200	15,600	2,620
Mar. 1– 2	(352.0)	8½	15½	0.0	8	....	9.6	8,800	12,500	2,090
Mar. 2– 3	338.2	12	12	0.0	32	....	4.6	7,800	11,500	1,900
Mar. 16–17	352.8	11	13	7.0	0	23	21.7	11,600	16,400	2,740
Mar. 17–18	(352.8)	10½	13½	7.0	0	....	22.0	11,400	16,200	2,700
Mar. 18–19	(345.8)	7½	16½	0.0	8	....	21.6	8,300	12,000	1,990
Mar. 19–20	339.0	8	16	0.0	32	....	22.3	7,000	10,300	1,700
Apr. 14–15	362.8	13½	10½	7.0	0	22	22.9	11,500	15,800	2,670
Apr. 15–16	(355.8)	4	20	0.0	8	....	21.8	7,600	10,700	1,790
Apr. 16–17	350.4	6½	17½	0.0	32	....	21.7	6,700	9,600	1,590
May 4– 5	346.6	9½	14½	3.5	0	23	22.6	7,800	11,300	1,860
May 5– 6	(346.6)	9½	14½	3.5	0	....	22.1	7,700	11,100	1,840
May 6– 7	(343.2)	7½	16½	0.0	24	....	22.2	5,400	7,900	1,300
May 7– 8	339.0	9½	14½	0.0	48	....	22.0	5,500	8,100	1,330
Steer F:										
Dec. 17–18	435.2	9	15	7.0	0	23	22.5	11,900	13,700	2,470
Dec. 18–19	(435.2)	11	13	7.0	0	....	22.3	11,900	13,700	2,470
Dec. 19–20	(428.2)	9½	14½	0.0	8	....	22.4	9,300	10,900	1,950
Dec. 20–21	415.8	7½	16½	0.0	32	....	21.3	8,100	9,700	1,730
Jan. 19–20	408.6	14	10	3.5	0	24	21.9	9,200	11,300	1,990
Jan. 20–21	(408.6)	10	14	3.5	0	....	22.2	8,800	10,800	1,900
Jan. 21–22	(405.2)	10	14	0.0	24	....	22.3	7,100	8,800	1,540
Jan. 22–23	399.6	10½	13½	0.0	48	....	21.7	6,500	8,100	1,420
Feb. 13–14	394.6	13	11	3.5	0	13	9.2	9,400	11,900	2,070
Feb. 14–15	(391.2)	11	13	0.0	24	....	10.2	7,500	9,600	1,660
Feb. 15–16	383.2	12	12	0.0	48	....	10.6	7,000	9,100	1,570
Mar. 23–24	423.2	13½	10½	7.0	0	25	22.1	12,500	14,800	2,640
Mar. 24–25	(423.2)	10½	13½	7.0	0	....	22.5	12,600	14,900	2,660
Mar. 25–26	(416.2)	9½	14½	0.0	8	....	22.7	9,100	10,900	1,940
Mar. 26–27	399.8	10½	13½	0.0	32	....	22.2	7,700	9,600	1,680
Apr. 20–21	424.0	11	13	7.0	0	21	22.5	12,300	14,500	2,590
Apr. 21–22	(424.0)	11½	12½	7.0	0	....	22.3	12,300	14,500	2,590
Apr. 22–23	(417.0)	9½	14½	0.0	8	....	23.3	8,700	10,400	1,860
Apr. 23–24	(410.0)	(3)	(3)	0.0	32	....	21.7	7,500	9,100	1,620
Apr. 24–25	[4] 404.2	[4] 8	[4] 8	0.0	56	....	22.4	7,600	9,400	1,650
May 11–12	407.0	12½	11½	3.5	0	21	22.0	9,100	11,200	1,970
May 12–13	(407.0)	13	11	3.5	0	....	23.2	9,000	11,100	1,950
May 13–14	(403.5)	8½	15½	0.0	24	....	22.7	6,300	7,800	1,370
May 14–15	392.6	11	13	0.0	48	....	21.7	6,200	7,900	1,370

[1] Beginning and ending at 4h 30m p. m.

[2] Timothy hay fed to both steers, until Mar. 6, 1925, in the case of steer E, and Mar. 9, 1925, in the case of steer F; alfalfa hay fed thereafter.

[3] Records incomplete for 24 hours.

[4] Experiment only 16 hours long. Data computed to 24-hour basis.

assessment of the quantitative degree of activity has been made for each of the different experimental periods. In discussing the result we shall therefore be able to state with considerable confidence whether the activity was materially different on the different days of the experiments. Complete records with regard to the number of hours spent in lying and standing were also secured and are given in Table 53.

The two animals used for this work were essentially of the same age and size, although steer E was actually somewhat smaller than steer F, weighing 369 kg. at the beginning of the series of experiments as compared with steer F's weight of 435 kg. Both animals, in the period from December 1924 to May 1925 lost about 30 kg. as a result of the winter's experimental régime, which included 13 or 14 intermittent fasting days. A general effort was made between the fasts to make up in part for the lost feed, but it is clear that there was not complete compensation, as is shown by the loss in body-weight.

Influence of Quantity and Character of Ration Upon Metabolism During Feeding

These 4-day experiments were made primarily to study the effect of fasting upon the metabolism, but, in the attempt to establish standard feeding conditions prior to the fasting, information was also secured regarding the metabolism during maintenance and submaintenance feeding with two different kinds of hay, timothy and alfalfa. Their influence upon the metabolism is of special interest, owing to the great economic problems involved in the rationing of domestic animals. It is not our purpose, however, to enter into an extensive treatment of the economic value of these two feedstuffs, for the feeding experiments were not made primarily with this in view. The observations are of significance, however, in indicating the nutritive plane of the animal prior to the complete withdrawal of food and furnish a base-line for the study of the effect of fasting.

In Table 53 the values for the total heat-production per 24 hours have been recorded, but since steers E and F differed somewhat in weight, this discussion will be confined to a consideration of the heat-production per 500 kg. of body-weight per 24 hours. The picture will be essentially the same with the heat-production per square meter of body-surface per 24 hours, but the consideration of these values will be deferred for later, more critical analysis from another point of view (see pp. 218 to 222).

The effect upon the heat-production of a maintenance ration of 7 kg. of hay was studied with steer E on four occasions. In two cases the ration consisted of timothy hay and in two cases of alfalfa hay. With steer F one experiment was made with a maintenance ration of timothy hay and two experiments were made with a maintenance ration of alfalfa hay. In all but one instance, i. e., on February 27 to March 1 with steer E, the environmental temperature was essentially 22° C., and for the moment, therefore, the effect of environmental temperature may be disregarded. When steer E was on a maintenance ration, the heat-production per 500 kg. of body-weight per 24 hours ranged from 15,300 to 16,400 calories, the higher values being noted with the alfalfa hay. With steer F the values range from 13,700 to 14,900 calories, the alfalfa hay again resulting in a higher heat-production. Both animals, therefore, have essentially a somewhat higher heat-production with the maintenance ration of alfalfa hay.

The smallness of our staff made it impossible to carry out complete digestion experiments and nitrogen metabolism experiments, and the metabolizable energy in these two different rations could not be determined. There is little, if any, reason to believe, however, that such determinations would materially alter the conclusions as presented, for we are dealing here with the heat-production, under the same conditions, of animals which are seemingly strictly comparable. It should be pointed out, however, that alfalfa hay is nitrogen-rich and timothy hay is nitrogen-poor, and that undoubtedly on timothy hay, and possibly on alfalfa hay, the animals were actually losing nitrogen.[a]

Since these experiments were planned primarily to note the effect of maintenance and submaintenance feed-levels and variations in environmental temperature upon the metabolism during feeding and fasting, the comparison of the influence of timothy and alfalfa hay was only an incidental study. The discussion of the influence of these hays upon the metabolism at the submaintenance level is therefore somewhat complicated by the fact that in these submaintenance experiments marked differences in temperature designedly prevailed. We will consider for the moment, therefore, only those submaintenance experiments in which the chamber temperature was not far from 20° C.

When a submaintenance ration of 3.5 kg. of either timothy or alfalfa hay was given, the metabolic level of both steers during feeding was lowered decidedly. Thus, we find that with steer E the 24-hour heat-production per 500 kg. of body-weight during feeding with timothy hay has changed from an average maintenance level of 15,800 calories on December 12–13 and December 13–14 to an average submaintenance level of 11,500 calories on January 13–14 and January 14–15. With alfalfa hay, the metabolism has fallen from a maintenance level of 15,800 calories on April 14–15 to a submaintenance level of 11,200 calories on May 4–5 and May 5–6. With steer F the 24-hour heat-production per 500 kg. of body-weight during maintenance feeding on timothy hay was 13,700 calories on December 17–18 and December 18–19, but fell with submaintenance feeding to an average of 11,000 calories on January 19–20 and January 20–21. With alfalfa hay the maintenance level in April was 14,500 calories and the submaintenance level in May was 11,200 calories.

From these data it can be seen that the submaintenance level of metabolism was much lower than the maintenance level in the case of both steers. Moreover, the submaintenance level of metabolism was essentially the same with both steers, regardless of the character of the hay, but since the maintenance level of metabolism of steer E was greater than that of steer F, the fall in his metabolism to the submaintenance level is somewhat more pronounced. The fall in metabolism with both steers is slightly greater with alfalfa than with timothy hay. In view of the well-known difficulties of

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[a] Armsby and Fries, (U. S. Dept. Agric., Bureau Animal Industry Bull. 51, 1903, p. 9) found that timothy hay was too poor in protein to be used as a maintenance ration and added linseed meal to the ration.

making direct comparisons of the heat-production of animals with which digestion experiments are not simultaneously carried out, conservative treatment of these findings is necessary. In the submaintenance experiments, undoubtedly both animals were losing nitrogen heavily. From our earlier research on undernutrition in steers, in which we found that submaintenance feeding did not materially alter the digestibility of the ration,[a] it is assumed, however, that the digestibility of the feed remained essentially the same as it was when the steers were on maintenance rations.

INFLUENCE OF QUANTITY AND CHARACTER OF RATION UPON METABOLISM DURING FASTING

For the study of fasting *per se,* the metabolism measurements on the two days of fasting in the several experiments claim our greatest attention. Considering again the heat-production per 500 kg. of body-weight, we note that as usual in all of the experiments the heat-production on this basis decreased markedly on the fasting days and was in general lower on the second of the two days. From our analysis of the data for the longer fasts, however, it is obvious that a still further reduction in the heat-production would occur if the fast were prolonged beyond two days, and that undoubtedly at the end of two days the period of true fasting (i. e., when the contributions from the feed residues in the intestinal tract would have practically ceased) has not yet been reached.

The metabolism on the first day of fasting following submaintenance feeding was lower than that following maintenance feeding. According to the experimental plan in these 4-day experiments, however, the first day of fasting following maintenance rations represents a period beginning 8 hours after the last feed and continuing until 32 hours after the last feed. Following submaintenance rations, it represents a period beginning 24 hours and continuing until 48 hours after feed. These differences in the time represented by the first day of fasting are due to the differences in feed-level. Thus, in the submaintenance experiments, feed was given only once a day and at such a time during the day as to bring the beginning of the third experimental day (or the first day of fasting) 24 hours after the last feed. In the maintenance experiments the feed was given twice a day, and the first day of fasting therefore began only 8 hours after feed. It is important to bear this in mind in the interpretation of the results, for in the submaintenance experiments the fasting-period is distinctly longer than in the maintenance experiments. Hence the markedly lower metabolism found on the first day of fasting in the submaintenance experiments may be in part accounted for by the fact that this day represents a later period in the fast than does the first day of fasting in the maintenance experiments.

The influence of the character of the hay upon the actual fasting metabolism at the different nutritive levels may best be compared by considering only those experiments in which the environmental temperature is similar. On the first day of fasting after maintenance feeding with timothy hay the heat-production of steer E per 500 kg. of body-weight is 12,300 calories. This drops on the second day to 11,000 calories. Under similar conditions with alfalfa hay, the metabolism is 12,000 calories on the first day of fasting

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 131.

and drops to 10,300 calories on the second day. The decrease is thus 1,300 calories in the first case and 1,700 calories in the second case. In a second experiment with steer E with alfalfa hay (April 14 to 17) the decrease is 1,100 calories from the first to the second day of fasting.

With steer F there was a drop of 1,200 calories from the first to the second day of fasting in the December fast, following a maintenance ration of timothy hay. In the March fast following the maintenance ration of alfalfa hay there was a decrease of 1,300 calories, and in the April fast under the same conditions a fall of 1,300 calories. In this latter fast the metabolism was also measured for the first 16 hours of the third day of fasting, and has been computed to the 24-hour basis. No appreciable difference in metabolism, however, is to be observed between the second and third days of fasting in this April fast with steer F.

In general, distinctly lower values are found on the two fasting days following maintenance feeding with alfalfa hay than following maintenance feeding with timothy hay.

In the submaintenance experiments at or about 20° C., essentially the same metabolism per 500 kg. of body-weight was noted during the two feed days, with both hays and, indeed, with both animals, i. e., not far from 11,000 calories per 24 hours. On the first day of fasting, that is, 24 to 48 hours after food, steer E had a metabolism of 9,800 calories following the submaintenance ration of timothy hay and 7,900 calories following the ration of alfalfa hay. With steer F the corresponding figures are 8,800 calories and 7,800 calories, respectively. Thus, both animals have a strikingly lower level of metabolism following a submaintenance ration of alfalfa hay. On the second day of fasting, in the same series of experiments, steer E had a heat-production of 9,000 calories following the submaintenance ration of timothy hay in January and 8,100 calories following the alfalfa hay. Steer F produced 8,100 calories on the second day of fasting following a submaintenance ration of timothy hay in January and 7,900 calories following a submaintenance ration of alfalfa hay in May. There is therefore also a distinctly lower metabolism with both of these animals on the second day of fasting at the submaintenance level with alfalfa hay. It is to be observed, however, that in the May experiments with both animals, essentially the same values were noted on the two days of fasting, there being a slight rise on the second day.

The general picture of the influence of the two different feeds upon the fasting level of metabolism, in experiments at environmental temperatures ranging close to 20° C., is that the fasting metabolism of both animals was decidedly lower after alfalfa hay than after timothy hay and that this relationship persisted into the second day of fasting. Thus we have clear evidence that following a ration of alfalfa hay, the nutritive level of the animal calls for a fasting metabolism actually less than that following a ration of timothy hay, whether the ration is a maintenance or a submaintenance one. It is obvious that for the complete control of this finding, experiments are highly desirable in which it is clearly established that the animals are in nitrogen equilibrium on the full maintenance ration. On submaintenance rations nitrogen loss is inevitable.

Influence of Environmental Temperature

Our earlier results on the influence of environmental temperature were, on the whole, of such nature as to warrant the conclusion that the temperature of the environment has no material influence on heat-production under ordinary conditions, although some of the data did suggest that with the lower temperature there was actually less heat produced. In the series of 4-day experiments reported in Table 53, there is clear-cut evidence of a pronounced influence of temperature upon the metabolism when the other factors which might influence the metabolism remain essentially constant. This is particularly true in the case of the submaintenance experiments in January and February with steer E, when timothy hay was fed. The second of these two experiments was made at a much lower temperature (on the average nearly 17 degrees lower) than the first, and the heat-production per 500 kg. of body-weight was actually considerably higher at the lower temperature. Thus, on the first two days with feed at the higher temperature of 22° C. the heat-production was 11,700 and 11,200 calories per 500 kg. of body-weight. When the temperature was 4.7° and 5.1° C., respectively, the heat-production on the two feed days rose to 13,300 and 13,600 calories, an increase of approximately 17 per cent. On the first day of fasting following the submaintenance ration the heat-production per 500 kg. of body-weight was 9,800 calories at the higher temperature and 10,800 calories, or 11 per cent higher, at the low temperature of 5.7° C. On the second fasting day the metabolism was 9,000 calories at 22.6° C. and 10,100 calories at 8.8° C., or 12 per cent higher. These experiments show definitely, therefore, that the influence of environmental temperature at the submaintenance level is noticeable, and that a difference of 17 degrees in the temperature has made a difference of not far from 17 per cent in the metabolism, i. e., a difference of 1 per cent in the metabolism for a change of 1° C. in temperature. The picture is not materially altered when the heat-production is computed per square meter of body-surface, the cold temperatures resulting in distinctly higher values.

With steer F, a comparison of high and low environmental temperatures was likewise made in connection with his two submaintenance experiments in January and February, with timothy hay. In the January experiment the average chamber temperature was about 22° C. and in the February experiment it was about 10° C. The difference in temperature was therefore not so great as in the case of steer E, and the experiment at the lower temperature included only one day, February 13–14, with feed. On this day the heat-production per 500 kg. of body-weight was actually 7 per cent higher than the average heat-production on the two feed days in the January experiment. On the first day of fasting the metabolism at the lower temperature was 9 per cent higher and on the second day of fasting 12 per cent higher.

With the two animals the picture of the influence of environmental temperature under submaintenance conditions is essentially the same. The effect is, however, apparently not proportional to the difference in temperature, at least so far as can be judged from experiments with two different animals, for in the case of steer F the influence of a change in temperature of approximately 12 degrees (the lowest temperature reached being only about 10° C.) was essentially the same as that noted with steer E, which was subjected to a difference in temperature of 17 degrees (the lowest temperature being about 5° or 6° C.). Such meager data do not permit of drawing many conclusions, and it is probable that no definite mathematical relationship can be established, such as has been suggested frequently in the literature, i. e., that each degree fall in temperature results in a certain definite (percentage) rise[a] in metabolism.

Pronounced temperature differences did not exist when the animals were on alfalfa rations, either at the maintenance or submaintenance level of nutrition, as the season was too far advanced for low temperatures. During maintenance feeding with timothy hay, however, two experiments with steer E are available, one in December and one in February, for a study of the effect of low and high temperatures. In these two experiments, the influence of the environmental temperature is entirely different from that when the steer is on submaintenance rations. In the December experiment the average chamber temperature was 22.3° C. and in the February experiment it varied from 3.6° to 9.6° C., being on the average about 6° C. The difference in temperature was thus essentially 16°. On the two feed days, when 7 kg. of timothy hay were eaten daily, the heat-production per 500 kg. of body-weight was 16,000 and 15,600 calories at the high temperature and 15,300 and 15,600 calories at the low temperature. In other words, there was essentially no difference in the metabolism, except for a slightly lower value on the first of the low temperature days. On the first day of fasting the metabolism at the high temperature was 12,300 calories as compared with 12,500 calories at the low temperature, there being an inappreciable increase on the cold day. On the second day of fasting the metabolism was 11,000 calories as compared with 11,500 calories, the increase being 5 per cent at the low temperature. On the basis of the heat-production per square meter of body-surface, the increase was 70 calories or 4 per cent on the second fasting day. Thus, although with the low environmental temperature there is seemingly an increase in the heat-production on the second fasting day, the heat-production on the two food days is practically constant regardless of the temperature, or in one instance is slightly lower at the low temperature. One may therefore conclude that the difference in temperature has practically no effect upon the metabolism when the steer is on a maintenance ration of timothy hay. It is somewhat surprising that the difference is not greater on the second day of fasting than was actually found. From the evidence in the submaintenance experiments, where the lower nutritive plane renders the animal seemingly more susceptible to the environmental temperature, so that there is a demand for a greater heat-production at the lower temperature, one would have expected in the fasts following maintenance feeding a greater heat-production than is actually recorded on the second day of fasting at the low environmental temperature.

The conclusion drawn from these data that a low environmental temperature frequently has no influence upon the metabolism is fully in line with

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[a] Recently, Capstick and Wood (Journ. Agric. Sci., 1922, 12, p. 257) found with swine that as the environmental temperature decreased below the critical temperature (21° C.), the heat loss increased at the rate of about 4 per cent per degree.

the findings in the excellent research of Magee, who studied the influence of variations in the external temperature upon the energy exchange of the goat.[a] Magee found that between 13° and 21° C. the metabolism is essentially constant. Below 13° C. it rises only slightly, but as the temperature passes above 21° C. a pronounced gradual increase in the metabolism is observed.

Influence of Lying and Standing

The computation of the heat-production per 500 kg. of body-weight and per square meter of body-surface in these 4-day experiments represents an attempt to equalize the differences in the body-size of the animals so that the values for the different days of each experiment, and particularly the values for the different animals, may be compared with each other. A still further attempt to reduce the values to a more comparable basis would be to compute the heat-production on the basis of uniformity in standing and lying.[b] Several methods of making this computation have been proposed, all of them based upon too few experimental data. Our own observations on the difference in metabolism in the lying as compared with the standing position, although extensive, are not sufficiently extensive to be fully convincing. The information secured in our earlier experiments was contaminated by irregularity in the movements of the animal, the uncertainty as to when the animal would lie down or stand up, and the inclusion in the lying period or in the standing period of the effort of getting down or of rising. Since the conclusion of the fasting experiments with our four steers, however, we have been able to obtain some clear-cut comparisons of the metabolism during standing and lying, in experiments in which the effort of changing from one position to the other has been ruled out. In many of these experiments we observed that the difference in position resulted in a difference of from 20 to 30 per cent in the metabolism on days with feed, but that there was a tendency for this difference to diminish during fasting and practically to disappear after the second or third day of fasting. In other experiments, a difference in the metabolism of as much as 20 per cent due to difference in body position persisted even to the fourth or fifth day of fasting, although there were occasionally 8-hour periods when the difference almost disappeared. It seems highly probable that the correction for the difference in position is somewhat greater than that reported by Forbes, Fries, and Kriss[c] (see p. 211). Pending further information on this point, however, the values in Table 53 for the 24-hour heat-production during the series of continuous 4-day experiments have not been corrected to a standard day of 12 hours standing and 12 hours lying.

It is obvious that these experiments, by their very nature, represent that period of an animal's existence when the greatest influence of the activity of standing and lying is to be found, comprising as they do two days on feed and two days of fasting. Undoubtedly, the heat values would be somewhat lower had they been determined exclusively when the animal was

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[a] Magee, Journ. Agric. Sci., 1924, 14, p. 506.

[b] Fries and Kriss, Am. Journ. Physiol., 1924, 71, p. 60.

[c] *Ibid.;* Forbes and Kriss, Journ. Agric. Research, 1925, 31, p. 1085.

lying. Differences in muscular activity necessarily occur, however, during a 24-hour day, especially when the animals are searching for and expecting food. Such activity has been noted in the records of the number of hours spent in standing and lying during the day, and, in addition, a relative estimate of the degree of activity from day to day has been obtained from the kymograph records. These records show that in general the activity was not very great. Assessing the degree of activity as indicated on the kymograph records on the crude basis of minimum (activity I), moderate (activity II), and excessive (activity III) activity, we would say that in many instances activity II occurred on the two feed days. This activity is to be expected, since the animals were eating, digesting their feed, and ruminating. The activity on the two fasting days, however, was usually somewhat lower than on the two feed days· Undoubtedly, therefore, the metabolism on the first two days with feed was influenced by a greater degree of stall activity than the metabolism on the two fasting days. Only when the animal is lying is the muscular activity reduced to a minimum. Indeed, one might argue that if the animal remained absolutely quiet when standing, the metabolism would not be much greater than when lying. This argument is in part borne out by the fact that as the fast progresses and the animal becomes less restive while standing, the difference in metabolism due to the difference in body position tends to disappear. (See pp. 211 to 213.)

The Basal Metabolism of Steers

With humans it is argued that the metabolism measured 12 hours after the last food and during complete muscular repose is the so-called "basal metabolism" and that for comparative purposes it is permissible to compare the metabolism of one individual measured under these conditions with that of another individual measured under the same conditions. Usually these determinations are made in short periods and are supposed to represent the minimum metabolism. The metabolism as thus determined is not, however, the irreducible minimum, for undernutrition, fasting, and sleep may result in an even lower metabolism. From the standpoint of physiology, it is important to measure the metabolism of various living organisms under as nearly as possible constant conditions, in order to have a suitable basis for the comparison of different individuals of the same and different species.

It is impossible to secure complete muscular repose with ruminants, for they are not cooperative. They can be forced to stand by hitching a chain under the neck, but this procedure is ineffective after several hours, as they become very restless and irritable under prolonged restriction. They will not remain in the lying position for any definite length of time, and even when they are lying there may be more or less movement of the body and particularly the head. It would be ideal to measure the basal metabolism of ruminants only when they are in the lying position and quiet. This is usually impracticable, however, and the metabolism must be measured under the conditions of stall activity, in which the animal has freedom to rise or lie down at will and to perform those minor muscular movements permitted by the rather narrow confines of the stall, though restrained by the usual stanchion. The sum total of such activities is reasonably uniform from day to day, however, as is strikingly shown in the continuous 4-day respiration experiments with steers E and F, in which it was noted that during the two days on feed the total 24-hour metabolism was almost always the same on any two succeeding days.

With humans and carnivorous animals the food in the intestinal tract is fairly rapidly absorbed. Immediately after the ingestion of food there is a rise in the metabolism, but if no more food is taken, the metabolism gradually decreases and after 12 hours a plateau is reached which persists probably for 12 or more hours, during which time there is only an insignificant alteration in the metabolism. Further abstinence from food results in a lowered metabolism, and with prolonged fasting the metabolism falls off appreciably. In the case of large ruminants there are large masses of feed residues in the alimentary tract, which are absorbed only slowly, and even after food is withheld, this intestinal content may contribute to the metabolism of the animal for some time by furnishing energy from material either directly absorbed or elaborated by fermentative processes.

Prior to our study of undernutrition in steers, few respiration experiments had been made with large ruminants in which feed was withheld for any length of time. In our research on undernutrition, the metabolism of all of the steers was measured for comparative purposes 24 hours after the last food. In a few instances in 1919, measurements were made 50 or more hours after food.[a] It was early recognized that although the digestion of ruminants has by no means completely ceased 24 hours after the last feed, the active peak of digestion has passed. Recent determinations of the methane production of cattle in Armsby's laboratory[b] indicate that even during the second 24 hours of fasting the methane production is relatively high and, though it falls off rapidly during the first three days after feed, it is not until the sixth or seventh day of fasting that the production is as low as 2 or 3 gm. per day. Without doubt the methane production is a fair index of the total digestive fermentation, but it is questionable whether digestive activity as such has not essentially ceased even before the great decrease in methane production takes place.

Although the stall confinement of cattle during respiration experiments makes the degree of muscular activity during any comparative series of metabolism measurements, especially during 24-hour periods of measurement, more or less uniform, it is almost impossible to secure a sharply defined post-absorptive state in the ruminant. Experimental study is therefore necessary to determine whether a fairly definite plateau of metabolism is reached after the peak of digestive activity has passed, corresponding to that noted with humans 12 hours after the ingestion of food.

Incidence of Plateau in Metabolism of Steers after Cessation of Active Digestion

In our series of long fasts (see Tables 48 to 50, pp. 173 to 178) it was pointed out that the heat-production, expressed on any of the usual three bases of computation, decreases rapidly on the second day of fasting, that is, the period beginning 42 to 56 hours after the last food. There is fre-

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, Table 55, p. 210.

[b] Braman, Journ. Biol. Chem., 1924, **60**, p. 85.

quently a further decrease on the third day. An examination of the figures in Table 49 (p. 176), leaving out of consideration the submaintenance experiments in March 1924, with steers C and D, and the submaintenance experiments with steers E and F, shows that in 12 experiments with steers C and D approximately a plateau in metabolism was reached on the second day in 4 cases, on the third day in 6 cases, and on the fourth day in only 2 cases. Hence it would seem as if in general on the third day, that is, during the 24-hour period beginning between 65 and 80 hours after food, a fairly uniform metabolism would be found, which would not be rapidly altered during the following 24 or 48 hours, although the tendency for a continuous decrease in metabolism with prolonged fasting is obvious. It should be borne in mind, however, that the data given in Table 49 were secured from only three or four half-hour periods of measurement, usually in the forenoon, and in at least two cases the animals had just come in from pasture. In the other cases, they were presumably at a maintenance level of nutrition, but since their body-weights were somewhat different in the different experiments, they were not necessarily in the same state of nutrition in all experiments. Furthermore, the metabolism of steer D, on the whole, was higher than that of steer C, in large part accounted for by the fact that steer D was almost invariably somewhat more restless.

In the continuous 3-day experiments with steers C and D (see Table 52, p. 186) the average heat-production of steer C per 500 kg. of body-weight per 24 hours was practically uniform on the three successive fasting days, being 8,100, 8,000, and 7,900 calories, respectively. The first value represents a period between 24 and 48 hours after food, or the period beginning 24 hours after the last food. This period is essentially the same as that represented by the first day of fasting in the fasts of 5 to 14 days (see Table 49), but the value of 8,100 calories is measurably lower than the average value found with steer C in the longer fasts. The same may be said with regard to steer D. His heat-production on the three successive days was 9,300, 9,200, and 9,200 calories, i. e., perceptibly lower than all except one value found on the first day in the long fasts, namely, 8,500 calories in the fast in April 1922. The subsequent values in the April fast, however, are also lower than the values found in the other long fasts. A possible explanation of this low value of 8,500 calories may be the possibility of error in the respiratory quotient, which was found to be 0.97 on this day, 32 hours after the last food. This was one of the first determinations of the respiratory quotient made with the new gas-analysis apparatus and, judged from other measurements made at approximately the same time after food, this value is distinctly high. If the quotient were lower, the value for the heat-production would be increased somewhat, possibly even to exceed the 9,300 calories noted in the fast in May 1924. Another, and perhaps more logical, explanation of this low value in the fast of April 1922, inasmuch as it would at the same time account for the low values on the three subsequent days, is that at the time of the fast in April 1922 steer D was distinctly in an undernourished condition. He had been through two fasts during the winter, a 10-day fast three months before, and actually weighed 621 kg. at the beginning of the fast in April 1922, as compared with 664 kg. on May 14, 1924.

Judging from the four continuous 3-day fasting experiments in 1924, if one begins the experiment 24 hours after the last food, and the previous ration has been a maintenance ration, the metabolism per 500 kg. of body-weight on 3 successive days is essentially the same. Thus, one would be justified in saying that a post-absorptive condition, or essentially a post-absorptive condition, was obtained with the steer on a maintenance ration of hay alone in a period beginning 24 hours after food was withheld, in other words, a period twice as long as that ordinarily assumed for man. Judging from the longer fasts, however, the plateau in metabolism occurs on the second or even the third day, rather than on the first day, i. e., 24 hours after the last food. A strict comparison of the data in these two series of fasts is complicated, however, by the fact that in one series the animals were measured while standing and for only three or four half-hour periods, and in the other series they were allowed to lie or stand at will and the periods of measurement were 8 hours long. Therefore, direct comparisons, without correcting for these differences of conditions, can not be made.

The conclusion as to the incidence of a plateau in metabolism following the cessation of active digestion would seem to be better founded upon 24-hour experiments than upon short experiments of about 2 hours. Further evidence on this point is available in the experiments made on steers E and F from December 1924 to May 1925. In these experiments the metabolism was measured in 8-hour periods during two days of fasting following two days on feed, or during four days inside the respiration chamber. From an inspection of the 8-hour values we find that with steer E, in December 1924, a plateau in metabolism is reached in approximately 16 hours after the last feed. The time when the plateau in metabolism occurred in these 4-day experiments is recorded in Table 54, which shows that in general the plateau begins 24 hours or later after the last food has been consumed. In the submaintenance experiments it occurs in most cases somewhat later. This is strikingly at variance with what one would expect, for one would think that with the smaller intestinal content the effect of the previously ingested feed would pass off more rapidly and the plateau, instead of being delayed, would be more quickly reached. It was thought that striking changes in temperature might possibly have an influence upon the time when the plateau appeared. An inspection of the average chamber temperatures recorded in Table 54, however, shows that environmental temperature is practically without significance in this respect. From the series of continuous 3-day fasting experiments inside the chamber, in which the animals had previously been upon a maintenance level, it was inferred that 24 hours after the last food was given a plateau in the metabolism of the steers was reached which might be considered as comparable to the post-absorptive metabolism of man. This is in general confirmed by the 4-day experiments at the maintenance level, as seen from Table 54, but on the submaintenance level this period is evidently somewhat delayed.

The Metabolic Plateau of the Same Animal when Fasting Under Different Conditions

In the fasts of 5 to 14 days it was pointed out that a level in the fasting metabolism might not occur until the second or even the third or fourth day of fasting. Another point to be considered is that the metabolism was rarely the same with the same animal for the first day or even for subsequent days of these different fasts, since the prefasting conditions were different. Thus, excluding the experiment at the submaintenance level, the average 24-hour heat-production of steer C per 500 kg. of body-weight during four half-hour periods in the standing position ranged from 8,800 to 9,800 calories on the first day of fasting, i. e., 22 to 32 hours after food. With steer D the differences were even greater, the metabolism ranging from 8,500 to 12,000 calories. Similar variations are found on the subsequent days. During the first few hours following the time when the first feed is withheld, i. e., about 12 hours after the last feed, one expects considerable variability in metabolism, depending upon the nature and amount of the previous feed-level. Whether the plateau indicating approximately basal metabolism will be at the same level in all experiments when the animal is subsisting upon a maintenance ration becomes a vital point at issue. In the different fasts of 5 to 14 days with steers C and D, excepting those in March 1924, the level of the plateau did vary, although this may have been due to the fact that the rations preceding the fasts, which were supposedly maintenance, consisted of hay in some cases and grass in others.

TABLE 54.—*Incidence of plateau in metabolism after cessation of active digestion, in 4-day respiration experiments with steers E and F*

Steer and date of experiment	Feed-level	Time after food when plateau in metabolism seems to appear	Average chamber temperature
1924 to 1925			
Steer E:		*hrs.*	°*C.*
December	Maintenance	16	22
February	Do	24	6
March	Do	24	22
April	Do	24	22
January	Submaintenance	40	22
February	Do	32	6
May	Do	32	22
Steer F:			
December	Maintenance	16	22
March	Do	32	22
April	Do	24	22
January	Submaintenance	32	22
February	Do	32	10
May	Do	24	22

The 4-day experiments with steers E and F in 1925 furnish additional evidence on this point. Thus, the data for the 4-day experiments with maintenance rations indicate that in the 8-hour periods of measurement the level of the plateau may range from approximately 8,700 calories per 24 hours to 6,750 calories in the case of steer E, and from 8,700 to 7,650 calories in the case of steer F.[a] In other words, the so-called "basal metabo-

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[a] These values are calculated from the 8-hour periods of measurement and do not appear in Table 53.

lism," when once attained after withholding of food, is seemingly not constant with the same animal, even if he has previously been upon a maintenance feed-level. If these experiments at the maintenance level are subdivided, however, according to whether the animal had been receiving timothy or alfalfa hay, it is seen that the higher values occur following the ration of timothy hay and the lower values following the ration of alfalfa hay.

A submaintenance ration has been shown to lower the level of the fasting metabolism markedly. The most important evidence on this point is brought out by the fasts with steers C and D in March 1924, at the submaintenance level, when extraordinarily low values for both animals were found. Similarly with the younger steers, E and F, at a submaintenance level the heat-production per 500 kg. of body-weight per 24 hours on the first day of fasting in February 1924 was, respectively, 10,900 and 10,300 calories. These same animals, when fasting at a maintenance level in April 1924, that is, about six weeks after the submaintenance experiments in February 1924, had a fairly constant metabolism during three days, steer E of 13,600 calories and steer F of 12,700 calories. In other words, as was the case with steers C and D, the metabolism was materially lower on submaintenance rations and the two conditions represented plateaus at different levels. The 4-day experiments with steers E and F on submaintenance rations furthermore show that although the fasting metabolism is on a lower level than it was following maintenance feeding, the metabolic level is higher following the submaintenance ration of timothy hay than it is following the submaintenance ration of alfalfa hay.

Conclusions Regarding the Incidence and the Level of the Plateau in Metabolism of Steers

On the basis of all the data available, one can conclude that *with the steer on essentially a maintenance ration* a plateau of fairly constant metabolism begins in many instances 24 hours after the last food, depending somewhat upon the amount and nature of the food, and that this level will remain essentially constant for three successive days. In some instances, 32 hours are required, singularly enough especially in those cases where the steers were upon submaintenance rations. In all probability at the end of 48 hours the animal is in a condition which is comparable, at least, with the so-called post-absorptive state in humans. It is difficult to give an exact percentage valuation to the difference between the probable level of metabolism 24 hours after food as compared with that 48 hours after food, but undoubtedly the peak of digestion has been passed 24 hours after the last food and the measurements of metabolism at this time may certainly be used for comparative purposes. Whether it is justifiable to assume that with the average ruminant the metabolism determined 24 hours after the last food represents the basal metabolism is highly doubtful. In general, from our evidence one would say that the metabolism beginning 48 hours after food is withheld would be less liable to fluctuation during the following 48 hours than perhaps at any other point in the course of the metabolism.

According to the evidence secured in the long fasts with steers C and D and in the 4-day experiments with steers E and F, the level in the plateau of metabolism will vary with different seasons of the year and as a result of changes in the quantity and character of the rations.

Since with steers it is impossible to insure complete muscular repose, since it is difficult to secure complete cessation of digestive activity, and furthermore, since the digestive activity of ruminants is relatively very great compared with that of humans, it is debatable whether any attempt to secure the equivalent of basal conditions in man is necessarily advisable.

In all the foregoing discussion the conclusions have been based chiefly upon the heat-production per 500 kg. of body-weight per 24 hours. But since the surface area is a function of the body-weight, the conclusions may also be based, without the slightest change in phraseology other than that of numbers, upon the heat as computed per square meter of body-surface per 24 hours.

Computation of the Fasting Katabolism of Steers from Experiments on Two Different Feed-levels

The exact determination of the period of time following food intake when the metabolism should be measured for purposes either of comparing the basal metabolism of a ruminant with his metabolism immediately following the ingestion of food or of comparing the basal metabolism of one ruminant with that of other ruminants, other animals, or, indeed, man, is a matter of considerable importance. With man the metabolism 12 hours after the last meal is commonly used as the basis for the study of the influence of subsequently superimposed factors, such as food, muscular activity, and a warm or cold environmental temperature. To study the energy value of various cattle feeds it is also highly desirable to be able to superimpose the effect of the feed upon a metabolism determined under basal conditions.

Formerly it was considered that the basal or fasting katabolism could be computed by the simple process of measuring the metabolism of an animal when consuming daily a given amount of food, and subsequently determining the metabolism of the same animal when consuming approximately one-half of this amount of food. The difference in metabolism at the two feed-levels was ascribed to the difference in the amount of the ration, and the fasting katabolism was computed as a linear function of this difference. This method was first proposed and applied by Professor Armsby many years ago,[a] and was in large part based on his own conviction that the actual fasting katabolism of ruminants could not be determined definitely. In the spring of 1919, Professor Armsby visited the laboratory at Durham, New Hampshire, and having seen the excellent manner in which our large steers had withstood undernutrition for long periods of time and having learned that we had made all of our respiration experiments at least 24 hours after the last food, stated that he believed more prolonged fasting would be feasible and suggested that we continue our fasting period to the fiftieth hour. It is significant that a fasting experiment prolonged to 50 hours was made on May 5–6, 1919, i. e., at the time of his

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[a] Armsby, Principles of Animal Nutrition, New York, 1906, 2d ed., p. 378.

visit. At the same conference Professor Armsby expressed himself as being uncertain whether the method of computing the fasting katabolism from two different feed-levels was as sound as he had originally believed. This matter was touched upon in our report on undernutrition.[a]

Our experiments in which the fast was prolonged for 52 hours or more show, as is to be expected, that there is a decrease in the carbon-dioxide production, due to the fact that the respiratory quotient and the total metabolism gradually decrease. Even in cattle the after-effect of food apparently disappears rapidly, and the condition approximating the prerequisite for basal metabolism measurements with man, so far as the question of food ingestion is concerned, is attained with ruminants not far from 32 to 48 hours after food is withheld. Prolonged fasting will lower the metabolism still further, as was clearly shown with the man who fasted for 31 days[b] and as is shown in the fasts of 5 to 14 days with our steers. But for the specific purpose of finding an approximate base-line for cattle, to which the influence of the ingestion of food may be referred, and to establish, if possible, a basal katabolism of steers for comparison with other animals and humans, we obviously may not deal either with prolonged fasting or prolonged submaintenance feeding, for this latter factor is likewise shown to lower the metabolism pronouncedly. Indeed, the most ardent advocates of the surface-area law insist that normal conditions of nutrition should be maintained. A critical study of our fasting results suggests that with animals under approximately normal conditions of nutrition the withholding of food for 32 hours should give, so far as the influence of food is concerned, favorable conditions for approximating the basal level. Even then, as is seen from the metabolism measurements during the fasts of 5 to 14 days, large differences may occur in different experiments with the same animal, although the nutritive condition, ruling out of such comparison the experiments on a submaintenance level, may not be pronouncedly different. This finding is in common with that not infrequently noted with man, and speaks for an absence of strict uniformity in metabolism even with the same individual, when changes in age are ruled out.

The object of this report is not primarily to study the effect of the ingestion of food upon metabolism so as to make use of this base-line obtained 32 to 48 hours after food, but it is pointed out here that the results suggest that this seems to be a logical procedure. From the standpoint of comparative physiology it is important to compare the basal metabolism of the steer determined under these conditions with that noted with other animals, particularly man. Two decades ago there was an attempt, commonly attributed to Erwin Voit,[c] to suggest complete uniformity in the heat-production of all warm-blooded animals per unit of surface area. At that time almost no attention was given to the degree of muscular activity, a factor now known to be of great importance. The question of the presence or lack

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 257. We wish to explain here that although our statement in our earlier publication refers solely to a letter received from Professor Armsby, as a matter of fact several days' intimate conference with him in Boston and at Durham was the basis for our general statement of Professor Armsby's beliefs.

[b] Benedict, Carnegie Inst. Wash. Pub. No. 203, 1915.

[c] E. Voit, Zeitschr. f. Biol., 1901, **41**, p. 113.

of food in the stomach was also not seriously considered. The effect of environmental temperature was only incidentally noted, and the method for computing the surface area of the various species of animals was only in its earliest stages of development. Under these conditions, however, it was stated that throughout the entire animal kingdom the heat-production was seemingly uniform, amounting to approximately 1,000 calories per square meter of body-surface per 24 hours, when the animal was in a normal state of nutrition.

In 1918, Armsby, Fries, and Braman[a] published a comparison of the basal katabolism of cattle and other species, in which they pointed out the difficulties of measuring or computing the basal katabolism of cattle. By comparing the total metabolism on two different amounts of the same feed and noting the increment in the heat-production per kilogram of dry matter of the feed, they computed indirectly the 24-hour basal katabolism of a number of cattle. Since they found a great difference in the heat-production according to whether the animal was lying or standing, they compute their basal katabolism data upon three different bases, namely, that the animal was lying for 24 hours, standing for 12 hours and lying for 12 hours, and standing the entire 24 hours. On the basis of 24 hours lying, the average computed basal katabolism of their cattle was 964 calories per square meter of body-surface per 24 hours. In determining the surface area of their cattle these investigators had the distinct advantage of using the more modern formula for surface-area measurements as suggested by Moulton,[b] but they had to determine the basal katabolism by the method of computation. This value of 964 calories they compare with the value of 935 calories found with men, 886 calories found with women in complete muscular repose, 1,078 calories with hogs, lying, and 948 calories with a horse, standing quietly. In their opinion this comparison confirms the conclusions of E. Voit.[c]

CORRECTION OF BASAL KATABOLISM TO A STANDARD DAY AS TO STANDING AND LYING

The Pennsylvania investigators computed that the basal katabolism of their cattle per square meter of body-surface, when the cattle were standing for the entire 24 hours, was 1,365 calories or 401 calories greater than when the animal was lying 24 hours. The increment due to the standing position is thus 41 per cent. It is perhaps unfortunate at this time to discuss the results of the Pennsylvania Institute of Animal Nutrition since Dr. Armsby's death, for evidently an extensive revision of calculations and factors is now being made. If the discussion is confined, however, entirely to their own published data, one is justified in pointing out several significant facts. In the first place, the difference of approximately 41 per cent between the metabolism in the lying and standing positions is, in accordance with the latest published and corrected computations from the Pennsylvania institute, very large, for the more recent figures of Fries and Kriss[d] would imply a difference of approximately 9 per cent. The standards

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[a] Armsby, Fries, and Braman, Journ. Agric. Research, 1918, **13**, p. 43.

[b] Moulton, Journ. Biol. Chem., 1916, **24**, p. 299.

[c] E. Voit, Zeitschr. f. Biol., 1901, **41**, p. 113.

[d] Fries and Kriss, Am. Journ. Physiol., 1924, **71**, p. 60.

of Fries and Kriss are derived from a series of experiments with one especially satisfactory animal, cow 874, which gave off 4.9162 calories per minute while standing and 4.4771 calories per minute while lying. The difference is 0.4391 calorie, which represents a decrease in the heat-production with a change in body position from standing to lying of about 9 per cent. Our own data regarding the difference in metabolism in the two positions are, as already stated (see p. 202), not extensive enough to permit of drawing definite conclusions, but on the basis of our results it seems highly probable that the correction factor might in general be nearer 20 than 9 per cent, with a probable influence of the length of time since feed was withheld.

Since this percentage correction plays an important rôle in the computation of the basal katabolism of cattle, when the computation is made on the basis of 24 hours lying, 12 hours standing and 12 hours lying, or 24 hours standing, it can be seen that the earlier reported values for the basal metabolism are immediately open to criticism. Since animals for the most part stand approximately 12 out of the 24 hours, the correction to 24 hours lying upon the old basis (41 per cent) is obviously too large, possibly 30 per cent too large on the basis of the 9 per cent difference indicated by the recent data of Fries and Kriss.

Møllgaard[a] has based a recent report on the metabolism of cattle in large part upon the method of calculation devised by Professor Armsby, but he does not make the correction for difference in body position. At the time of closing our report on undernutrition it was stated that we had only just received the report of Møllgaard with regard to the respiration experiments in his laboratory in Copenhagen. This report is, unfortunately, printed in Danish, although some of the table headings are in English and there is a short summary in English. We have therefore been considerably handicapped in analyzing his data, and it is more than likely that points raised in the following discussion may have been adequately cared for by Professor Møllgaard, whose keenness not only in scientific research but in the presentation of his results is well known by all who have come in contact with him. The experiments were made with the respiration chamber at Copenhagen. In this report we find no statement as to the environmental temperature, but in an English summary of his work[b] is the statement that all of his respiration experiments were made at an environmental temperature of 18° C. and as nearly as possible the same temperature was maintained in the stable (17.5° to 18.5° C.). Møllgaard's results do not confirm Armsby's conclusion that the metabolizable energy of a single feedstuff has a reasonably constant value. Møllgaard's treatment of the question of the influence of lying and standing is, however, of especial interest, although we have to differ strongly with one of his points of view in this respect. He concludes, from an examination of his metabolism

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[a] Møllgaard, Om Naeringsvaerdien af Roer og Byg til Fedning og om Naeringsstofforholdets Betydning for Fodermidlernes Naeringsvaerdi. Beretning 111, Forsøgslaboratoriet, Copenhagen, 1923, 159 pp.

[b] Møllgaard, New views regarding the scientific feeding of dairy-cattle. Compt. Rend. d. Travaux d. Congrès Internat. pour l'Élevage d. l'Espèce Bovine (The Hague): Internat. Cong. Rundveeteelt, 1923, p. 272.

measurements and the relative times that the animals are standing and lying, that the metabolism in the standing position is not independent quantitatively of that in the lying position, the increase in metabolism when the animal is standing being compensated by a corresponding decrease when it is lying down. "When the time of standing and the metabolism is computed for 24 hours, there is absolutely no correlation of long-time standing to high values of heat-production in respiration experiments on constant feed." As a result of these experiments, Møllgaard decides not to correct the metabolism to a uniform day of standing and lying.

Since the average stall experiments indicate that animals spend not far from 12 hours standing and 12 hours lying (although rather large differences are occasionally observed), the importance of this correction is not so great when the value of different feeds are being compared as it is perhaps in the theoretical discussion concerning the true fasting katabolism of animals, especially when this corrected value is to be compared with the measured basal metabolism of other warm-blooded animals, particularly man. The value of 26.34 calories per hour suggested by Fries and Kriss as the increase due to standing in the case of a 400-kg. cow, or the computed difference of 9 per cent, has the disadvantage of being determined upon only one animal. Another difficulty in attempting to correct for the difference in body position is the fact that the influence of the effort of getting up or lying down is frequently included in the comparative measurements. Obviously in determining the rate of metabolism in most of the practical problems, such effort is a legitimate part of the day's activity, although it should not be included in computing the basal katabolism.

INHERENT ERROR IN METHOD OF COMPUTING THE FASTING KATABOLISM FROM EXPERIMENTS ON TWO DIFFERENT FEED-LEVELS

In our study of undernutrition in steers, we found at no time values for the heat-production per square meter of body-surface as low as the 964 calories reported by Armsby, although the metabolic level was greatly lowered as a result of the submaintenance régime. Our measurements were, to be sure, always made with the steer in the standing position, and if the correction of 9 per cent were applied, our values for the measured heat-production per square meter of body-surface would be lowered by 9 per cent, to bring them presumably to the lying basis. With our submaintenance groups of steers, with which the lowest values were found between February 11 and May 2, the average heat-production per square meter of body-surface was not far from 1,460 calories in the submaintenance period.[a] If this value were reduced by 9 per cent to approximate the lying condition, the metabolism would be about 1,330 calories per square meter, even during this prolonged period of undernutrition. Indeed, if a 20 per cent correction is applied, the value remains about 1,200 calories. In the fasting experiments here reported it was found that the heat-production per square meter of body-surface, measured always in the standing position, ranged, for the

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, fig. 40, p. 292.

most part, around 1,700 calories on the day beginning from 42 to 56 hours after the last food, except in the case of undernutrition. But even with undernutrition a value of 1,600 or 1,700 calories was found with steers E and F. If these values were to be lowered by approximately 9 per cent, to bring them to the lying basis, they would still be around 1,450 to 1,550 calories, agreeing more closely with the value of 1,330 calories computed for the submaintenance experiments.

Additional evidence regarding the probable basal metabolism of steers is available in the experiments made between 50 and 53 hours after feeding with several of the steers used in our earlier submaintenance study.[a] The heat-production per square meter of body-surface per 24 hours has been computed in these instances from the carbon-dioxide production, an assumed respiratory quotient of 0.76, and a body-surface calculated from the formula $S = W^{5/8} \times 0.1081$ (see Fig. 8, p. 155). Application of the 9 per cent correction, to reduce the values to the basis of 24 hours lying, results in values ranging from 1,170 to 1,970, averaging about 1,550 calories.

It seems improbable that the metabolism of the steer 42 to 56 hours after food should not be approximating the basal condition. But even after the most prolonged fasting of 14 days the heat-production was about 1,400 calories per square meter of body-surface. If it were permissible to reduce this by 9 per cent to bring it to a basis of 24 hours lying, the heat-production would still be 1,270 calories at the end of this long period of fasting. Our evidence, therefore, points strongly to the fact that the basal katabolism of cattle is about 1,300 calories per square meter of body-surface per 24 hours, when the animal is lying the entire time.

In a recent article, Cochrane, Fries, and Braman[b] discuss the maintenance requirements of dry cows and use the method of computing the fasting katabolism by comparison of the effects produced by different amounts of the same feed. Computing the experiments on the basis of 12 hours standing and 12 hours lying, they present values for the fasting katabolism of 3 of their cows. If the surface areas of these cows are computed from their live weights by means of the curve in Fig. 8 (see p. 155) and if the reported values for the fasting katabolism are divided by the surface areas, the 24-hour heat-production per square meter of body-surface is found to be 857, 824, and 827 calories, or, on the average, 836 calories in the case of cow 886, 1,123 calories in the case of cow 874, and 1,079 calories in the case of cow 887. The authors have commented upon the differences between the values for the fasting katabolism, stating that cow 886 was extremely quiet, spending more than half of the experimental time in the lying position, that cow 874 spent about half her time lying quietly, but when standing was much more restless, and that cow 887 stood the greater part of the time and was more or less restless, even when lying. These experiments were computed on the basis of 12 hours standing and 12 hours lying. If the values were to be corrected to the basis of 24 hours lying, in order to compare them with the basal metabolism of man, they would all be reduced by

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, Table 55, p. 210.

[b] Cochrane, Fries, and Braman, Journ. Agric. Research, 1925, 31, Table XXII, p. 1078.

approximately 4.5 per cent. The average heat-production would then be 798 calories for cow 886, 1,073 for cow 874, and 1,030 calories for cow 887. These values are much more in accord with those computed by Armsby, Fries, and Braman in 1918. As a matter of fact, the average heat-production of cows 886, 874, and 887 would be 967 as compared with the average value for their group of animals of 964 calories.

These values are so at variance with our own findings, both in our earlier study of undernutrition and in this present study of fasting, as to suggest that a serious error inherent in the method of computing the fasting katabolism accounts for their low results. An analysis of the values for the actually observed heat-production of these same cows, 886, 874, and 887, published by Braman[a] in 1924, one year previous to the publication of the values for the computed fasting katabolism by Cochrane, Fries, and Braman, strengthens us in our conviction that the method of computing the fasting katabolism is in all likelihood at fault.

The minimum 24-hour heat-production of these cows, as measured in the calorimeter, was 6,061 calories. This value was found on the eighth and ninth days of fasting with one of the animals. Usually the heat-production during fasting was more nearly 6,500 calories, being somewhat lower on the second day than on the first day of fasting. On the fifth and sixth days in the case of cow 885 the total heat-production was 6,557 calories, or essentially the same as her metabolism earlier in the fast.

On the eighth and ninth days of fasting with two other animals, 6,061 and 6,302 calories are recorded. Information is not given as to the number of hours spent by the animals in standing and lying. Our own findings indicate, however, that, when fasting, animals are wont to spend more time in the lying than in the standing position. Thus, in the 4-day experiments with steers E and F (see Table 53, p. 195), on only one of the fasting days did the animal stand more than 12 hours, that is, on February 4–5, steer E stood for 17 hours and lay down for 7 hours. In our series of 3-day experiments (Table 52, p. 186) longer periods of standing were more frequently observed. For purposes of discussion, however, if one assumes that these heat values, as recorded by Braman, represent the metabolism during a day of 12 hours standing and 12 hours lying, they could be brought to the basis of 24 hours lying by being reduced approximately 4.5 per cent, granting that the difference between the metabolism during 24 hours lying and 24 hours standing is 9 per cent, as derived from the data of Fries and Kriss. On the other hand, if one assumes that the animals were standing the entire time, which is highly improbable, the reduction could be as high as 9 per cent. On this last assumption, and assuming an average fasting katabolism of 6,500 calories for cows 886 and 874, the corrected fasting katabolism would be approximately 6,000 calories. Since cows 886 and 874 weighed approximately 400 kg., their surface area would be not far from 4.7 square meters, according to the curve in Fig. 8 (p. 155). Their 24-hour heat-production per square meter of body-surface would therefore be approximately 1,280 calories, on the basis of 24 hours lying. The com-

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[a] Braman, Journ. Biol. Chem., 1924, 60, Table I, p. 82.

putation for the smaller cow 887, which weighed about 320 kg. and had an observed total metabolism of 6,061 calories, would give about 1,350 calories per square meter of body-surface per 24 hours.

This analysis leads us to believe that the true basal or fasting katabolism of these three cows is much more nearly 1,300 calories per square meter of body-surface than 967 calories, the average value derived from the fasting katabolism as computed from two feed-levels. Indeed, this average value of 1,300 calories is about 35 per cent higher than the computed fasting katabolism of these animals. Singularly enough, the article published by Cochrane, Fries, and Braman in 1925 gives no reference whatsoever to the fasting values reported by Braman in 1924, although we are inclined to think that this may possibly be due to a recognition of a necessity for some further revision. Our own experience with the effect of different feed-levels on fasting metabolism warrants the assertion that the fasting katabolism of cattle per square meter of body-surface per 24 hours is approximately 1,300 calories, save during prolonged fasting or fasting following extreme undernutrition. If the basal katabolism of cattle in the lying position is found to be as high as 1,300 calories, the comparison of this value with that commonly assumed for man and woman can be made only in full recognition of the fact that the cattle show a value approximately 35 or 40 per cent above that for humans, and this is entirely at variance with the hypothesis of E. Voit and his followers.

The fact that the computation of the fasting katabolism from experiments with two different quantities of the same feed gives results far lower than those noted when actual measurements are made of the fasting katabolism is due, we believe, to an inherent error in the experimental procedure. After the steer has been on submaintenance rations for some time, his metabolism would not represent strictly the metabolic effect of the submaintenance ration, since, as has already been stated, the metabolism at this point would also be profoundly lowered by the undernourished condition. The computation of the fasting katabolism from the metabolism at maintenance and submaintenance levels, therefore, gives results too low when the submaintenance metabolism is measured after the animal has begun to draw materially on its own body-tissue for support. In our own experiments, for example, the submaintenance ration was given for three or more weeks prior to the measurement of its effect. This procedure at the time was thought necessary on the conventional basis that the animal should be adjusted to the food-level and thus have a metabolism proportional to the food intake. The measurement therefore did not represent the effect of the reduced feed intake with the consequently lessened digestive activity and also the consequent decrease in intestinal fermentation, because the metabolism at this stage was materially altered by undernutrition, i. e., by drafts upon the body organism.[a] When feed is cut from

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[a] It has been definitely shown (Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923) that when the animal is forced to draw on his own body-tissue for support, the metabolism is depressed to an abnormally low level, since the animal parts with his own body-tissue, even for purposes of self-preservation, only with the limit of economy, all body activities being curtailed to save tissue.

maintenance to submaintenance there must be some point during the transitional stage of metabolism representing the basal condition before it is affected by undernutrition. From the previous discussion of the metabolic plateaus it would seem that this point could best be approximated during the second 24-hour period after feed reduction, an additional day being possibly added as a check. In other words, a 5-day respiration experiment, in which the first two days should represent maintenance, the third would represent a mixed effect, and the fourth and fifth days would represent the beginning of the submaintenance plateau (i. e., the level of metabolism as determined by the submaintenance ration before the effect of undernutrition has markedly manifested itself), appears to form the most logical method of procedure.

Whether the same difficulty would be found if the initial feed-level were above maintenance and the lower feed-level were at maintenance is still open for investigation, as our experiments were not made with this point in view. Since most studies in this field have been made upon the basis of maintenance versus submaintenance, it would seem that this explanation of the difference between the computed fasting katabolism and that actually existing with the animals may serve a helpful purpose.

From the data in the series of 4-day experiments with steers E and F, a study of a number of important problems outside of the field of fasting metabolism becomes incidentally available, such as the relative effect of reduction in food consisting of timothy or alfalfa hay. Thus, in the case of steer E, there apparently was a reduction in the total heat-production of about 3,500 calories as a result of reducing the ration from 7.00 kg. to 3.5 kg. of timothy hay. On the other hand, a reduction in the same amount of alfalfa hay resulted in a total daily reduction of 3,800 calories. With steer F, similar reductions resulted in a decrease of about 2,900 calories from timothy hay and 3,400 calories from alfalfa hay.

To make such a series of experiments complete, obviously a careful analysis of the digestibility of the hay and a determination of the nitrogen balance should be made. On the other hand, the extra precautions taken to secure uniformity of content of digestive tract during submaintenance feeding (in those experiments where the effect of curtailment of ration was compared with the effect of a full ration) by the conventional method of preparing the animal with a preliminary feeding-period of two or more weeks, undoubtedly resulted in a change in the nutritive level of the animal. This has been established by the comparative results of the various fasts. It would seem, therefore, as if the question of digestibility on lower rations should be studied independently and not combined with a study of the gaseous exchange. It is our purpose to discuss such data from these experiments as lend themselves to a study of these different angles later, as more information is secured not only upon steers but upon dry cows, with which we are at present carrying out observations. The data presented here are therefore primarily such as bear directly on the effect of the character and quantity of the previous feed-level and the effect of environmental temperature upon the fasting katabolism.

This discussion is of chief significance solely from the standpoint of comparative physiology. From the practical standpoint it may be assumed that in general a sufficiently close approximation of the fasting katabolism can be determined on animals, while standing, about 32 hours after the last food, and that if a satisfactory reduction in the measurement thus obtained is made for lying, the basal metabolism during 24 hours lying may be computed. This procedure should give a value which is suitable as a base-line in studies of the superimposed effects of various factors, provided the experiments are made shortly after this basal determination. The value will not be uniform with different animals, even if the metabolism is computed on the basis of surface area. It will not be uniform for the same animal at different times, particularly when there are profound changes in the nutritive state, for even with essentially the same nutritive state considerable differences do occur, as is seen in Table 48 (p. 173).

In consideration of the great difference between the fasting katabolism computed on the basis of the metabolism at two different feed-levels and that actually found by calorimetric and gaseous metabolism measurements during prolonged fasting, it would seem as if the computation method, at least in its present form, has limited value.

The Minimum Heat-production of Steers per Square Meter of Body-surface per 24 Hours

In the discussion of the plateau level in the metabolism of these fasting steers it was pointed out (see pp. 213 to 216) that the lowest level during fasting was about 1,300 calories per square meter of body-surface per 24 hours, i. e., higher than the conventional 1,000 calories ascribed to all warm-blooded animals as a class. An examination of all our values indicating the minimum heat-production per square meter of body-surface which may be expected with steers under numerous different conditions, irrespective of whether a plateau has been reached in the metabolism, becomes of interest for purposes of comparison with other researches made on this basis.

The lowest values for the 24-hour heat-production per square meter of body-surface occur in the series of experiments involving three or four half-hour periods of measurement. With steer C the lowest value is 1,060 calories on January 30, 1923, 49 hours after food. With steer D the lowest value is 1,190 calories, also the same number of hours after food and at about the same date, i. e., January 27, 1923. (See Tables 44 and 45, pp. 166 and 168.) In both of these instances the steers were at a maintenance level of nutrition. With steer C another low value of 1,100 calories was found on the second day of the fast in March 1924, following submaintenance feeding. With steer F, a younger animal, the lowest recorded value is 1,540 calories, 24 hours after the last food on February 19, 1924, which happened to be the first day after a fasting experiment. With steer E it was 1,520 calories on December 28, 1923, when the animal was upon a submaintenance level. (See Table 57, p. 232.)

In the continuous 3-day experiments in 1924, the heat values are based not upon three or four half-hour periods, but upon individual 8-hour periods. In this series the minimum heat-production of steer C was 1,580 calories on April 25, that of steer D was 1,820 calories on May 15, that of steer E was 1,890 calories on April 11, and that of steer F was 1,850 calories on April 1. (See Table 52, p. 186.) These measurements were all made while the animals were fasting, but immediately following maintenance rations. In the 4-day experiments in 1925, when the metabolism was also measured in 8-hour periods, lower values were found with the younger animals. Thus, steer E had a minimum 24-hour heat-production of 1,230 calories per square meter of body-surface in the 8-hour period beginning 32 hours after food on May 6–7, 1925, and steer F of 1,330 calories in the 8-hour period beginning 56 hours after food on May 14–15, 1925. In both instances the steers were fasting after a submaintenance level of nutrition.

The lowest values found with steers C and D were, therefore, 1,060 and 1,190 calories, and with steers E and F 1,230 and 1,330 calories, respectively.

A careful examination of the conditions under which these very low values for steers C and D were obtained brings out the fact that the metabolism of both animals had been measured at a very low temperature on one day and at a much higher temperature on the following day. Thus, with steer C on January 29, 1923, at a chamber temperature of 2.9° C., the heat-production was 1,740 calories per square meter of body-surface. On the next day the temperature of the chamber was raised to 24.9° C. and the metabolism per square meter of body-surface fell to 1,060 calories. With steer D the situation was similar, in that on January 26 the chamber temperature was 8.8° C. and the heat-production 1,850 calories, and on the next day the temperature was raised to 28.3° C. and the metabolism fell to 1,190 calories. In each case the second experiment at the high temperature was made 24 hours later than the first experiment, that is, 49 hours after food. As such large decreases in metabolism were not obtained with these steers during the first three days of fasting after full feeding in the series of long fasts, it is evident that these abnormally low values are the result of the pronounced effect of the sudden transition from a cold to a warm environment.[a] This conclusion is supported by another experiment with steer D on January 18 and 19, 1923. On the first day the chamber temperature was 3.4° C. and the metabolism was 1,730 calories per square meter of body-surface. On the next day the temperature in the chamber was raised to 28.2° C. and the metabolism fell to 1,290 calories. An examination of all our data shows that in practically every instance a striking rise in temperature resulted in a greatly lowered metabolism. When the temperature was 12° C. or above, however, the change in metabolism was no greater than would be expected on one or two successive fasting days.

This profound decrease in the metabolism of steers C and D, although apparently due to a sudden change of temperature, is difficult of further

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[a] A similar explanation does undoubtedly account for the low standard metabolism of 1,180 calories per square meter of body-surface per 24 hours noted with steer C on December 20, 1923, when on a maintenance ration. In this instance the steer had been for approximately 24 hours at a stall temperature of 3° C. and was then studied in the respiration chamber at a temperature of 19.5° C. (See Table 55, p. 226.)

explanation without other data on this point. The metabolism during the first day of fasting on the cold days, which was not far from 1,700 calories per square meter of body-surface, is not so high with these animals as, for example, on the first day of the long fasting experiments (see Table 50), and it is not indicative of an especially high metabolism produced by severe cold. The transition from the cold to the warm environment evidently had an immediate pronounced effect in lowering the metabolism, perhaps to be explained by the fact that prior to each metabolism measurement the animals had been in their metabolism stalls for only about 16 hours at a temperature essentially the same as that which prevailed in the respiration chamber during the experiment.

There are only a few instances where the conditions were reversed and the metabolism was measured at a high environmental temperature on the first day of fasting and at a low temperature on the second day. The most striking illustration is the experiment with steer D on February 2 and 3, 1923. On February 2 the chamber temperature was 27.9° C. and the heat-production was 1,610 calories per square meter of body-surface. The records of stall temperature show that from 8 p. m. on February 2 until the time of the respiration experiment on February 3 the environmental temperature was essentially 12° C. On February 3 the chamber temperature was 7.3° C. and the heat-production was 1,450 calories. In this instance the drop in metabolism was hardly more than would be expected with continued fasting, and the change in temperature apparently had no influence upon the metabolism. Because of these sudden changes in metabolism following a change in temperature, our plan of experimentation in studying the influence of environmental temperature was altered in the 1925 series in that the animals were kept for two weeks or more prior to an experiment at the specific temperature at which they were to be studied in the respiration chamber.

With humans there is almost no evidence to explain this pronounced lowering in metabolism with the change from a very cold to a warm environment. The Nutrition Laboratory has for many years been searching, without success, for some factor or combination of conditions that would result in a lowering of the so-called "basal metabolism" of humans. Profound undernutrition and fasting do lower it, but these are not immediate, superimposed factors. It has been maintained that a warm bath lowers the metabolism, and that the basal metabolism can only be secured when the body is immersed in water at about 35° C.[a] This problem was studied at the Nutrition Laboratory with several subjects, and it was noted that the metabolism was *not* lowered by immersion in the bath.[b] More recently Delcourt-Bernard and André Mayer have reported[c] that they have occasionally noted a very low metabolism with humans after prolonged immersion in a warm bath, indicating an after-effect of the bath. It is possible that with these steers in the somewhat rapid transition from the cold to

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[a] Lefèvre, Bull. Soc. Sci. d'Hygiène Alimen., 1922, **10**, p. 595.

[b] Benedict and Benedict, Bull. Soc. Sci. d'Hygiène Alimen., 1924, **12**, p. 541; ibid., Proc. Nat. Acad. Sci., 1924, **10**, p. 495.

[c] Delcourt-Bernard and Mayer, Compt. Rend., 1925, **92**, p. 62.

the warm environment there may be a period of relaxation or adjustment to the temperature, which may actually result temporarily in a lower heat-production. It is unfortunate that the tests of this after-effect of the warm environmental temperature were not prolonged sufficiently to note whether this low metabolism remained constant or whether there was a later reaction. This problem should be studied in the near future.

Of great importance to general physiology, however, is the fact that, at least with steers C and D, there are two instances of a heat-production per square meter of body-surface actually approaching 1,000 calories, the value commonly assumed to represent the heat-production of all warm-blooded animals. The fact that these values were found only under the special condition of an extreme change in temperature implies that we have to deal here not with a persistent level of basal metabolism but with a special, imposed condition, the effect of which, in all probability, is transitory. When steer C was subjected to submaintenance rations and then to prolonged fasting, the heat-production per square meter of body-surface was, to be sure, as low as 1,110 calories. But since this value reflects the influence of the superimposed effect of undernutrition, it can hardly be compared directly with values found with animals at a maintenance level of nutrition, even after they have undergone several days of fasting. Fasting *per se*, provided the initial level of nutrition has not been too greatly lowered by a submaintenance ration, results in a heat-production per square meter of body-surface per 24 hours much nearer 1,700 calories during the first 48 hours than the 1,060 and 1,190 calories noted with these two animals following the extreme change in temperature.

THE PHYSIOLOGICAL SIGNIFICANCE OF SURFACE AREA AND ITS RELATIONSHIP TO HEAT-PRODUCTION

For the comparison of the true basal metabolism of these steers with that of man, determined under the well-known prescribed conditions of the post-absorptive state and complete muscular repose, measurements made during periods of quiet lying, at least 48 hours after the last food, are presumably the best. Since all of our heat values were determined when the steers were standing or both lying and standing, they probably should be corrected for the extra effort of standing (see p. 211), if they are to represent conditions similar to those under which the basal metabolism of humans is measured. We have already seen (p. 214) that the average heat-production per square meter of body-surface of these steers 42 to 56 hours after food, which would correspond essentially to the 12-hour interval required with man, would be about 1,700 calories at the maintenance level and from 1,600 to 1,700 calories at the submaintenance level. If these values were corrected for the extra effort of standing, they would still be materially above 1,300 calories on the average.

This value of 1,300 calories per square meter of body-surface may therefore be taken as the probable basal metabolism or the lowest metabolism of these ruminants, which will remain reasonably constant for four or five days of fasting, after which the metabolism will fall off, as indicated in Table 50. The popular impression that the metabolism is 1,000 calories per square meter of body-surface for all warm-blooded animals must, we believe, be looked upon with great reserve in a refinement such as this. The basal metabolism of man has been found with considerable exactness to be, on the average, not far from 900 calories per square meter of body-surface. With these steers, however, the basal values are not far from 1,300 calories, or approximately 45 per cent higher.

The rectal temperatures of these steers were about 1 degree higher than the rectal temperature of the average man (37° C.). Physiologists, however, in considering this law of surface area and the heat-production per square meter of body-surface, are inclined to disregard differences in body temperature between species, although admitting that in the individual human small rises in temperature actually result in greater heat-production. Emphasis has been laid upon the matter of equal conditions of nutrition in comparing various animals. We have seen in our study of steers that the heat-production is lower at the submaintenance level than at the maintenance level, and that during fasting it is somewhat lower than at the submaintenance level. One of the most extensive uses to which the measured heat-production of man and the standard values are put, however, is the clinical application to pathological cases, in which undernutrition plays a large rôle. We have yet to see indications where differences in the nutritive states of humans have been seriously taken into consideration in assessing the measured heat metabolism and comparing it with normal standards.

The problem of establishing a basal heat-production with ruminants, which may be used for the comparison of the influence of the ingestion of various types of food and the influence of various levels of feeding, is by no means solved. Uniformity may not be hoped for with different animals. Differences with different feed-levels will undoubtedly be found. Differences with different environmental temperatures have already been noted, especially on the lower feed-levels. It is believed that a study of the reaction of an animal in a given nutritive state to the drafts upon body material, as exemplified by these short 2-day fasting experiments, and a study of the effect of various rations in enabling the animal to withstand such drafts upon body material when equal states of nutrition are assumed, may be of great value in estimating not only the nutritive states of an animal, but the actual value of various feeds to the animal for growth, maintenance, and protection against drafts upon body material.

Influence of the Ingestion of Food

The Immediate Reaction to the Ingestion of Food After a Prolonged Fast

In view of the difficulties experienced with humans during realimentation after a long fast or after a long period of undernutrition,[a] it was considered important to note the metabolic reaction of these steers to the ingestion of food after prolonged fasting. A number of respiration experiments were therefore made at the end of some of the long fasts, and the effect of the first feed following the fast was studied in continuous half-hour periods

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[a] Benedict, Carnegie Inst. Wash. Pub. No. 203, 1915, p. 49; Benedict, Miles, Roth. and Smith Carnegie Inst. Wash. Pub. No. 280, 1919, p. 683.

for from five to eight hours following the ingestion of feed, while the animal remained inside the respiration chamber. Information was thus obtained on the change in the respiratory quotient resulting from ingestion of food, and particularly on the change produced in the actual metabolism, as indicated by the carbon-dioxide excretion. From 1 to 2 kg. of chopped hay were usually offered to the steers, and in some cases a small amount of meal, not far from 1 kg.

In general, the animals were extremely slow about eating· When hay alone was offered they would take an hour or more to consume even a moderate amount, such as 1,000 to 2,000 grams. The grain, being more palatable, was apparently relished more and eaten with greater vigor. It would seem as if there was an instinctive control which retarded the steer from overeating. It was believed at first that a study of the immediate effect of feeding could be superimposed at the end of a fasting experiment, but the small amounts of hay consumed made such experiments unsatisfactory and almost without significance.

A comparison of the carbon-dioxide production on the last day of the fast with the carbon-dioxide production measured in the different half-hour periods of the respiration experiment made almost immediately after the animal had been fed, shows that during the first half-hour period there was invariably a striking increase in the metabolism. In the subsequent periods the carbon-dioxide production was irregular, with no clear indication of a continual increase during the 5 to 8 hours under investigation. There was always a pronounced rise in the respiratory quotient, which slowly though continually increased. The general conclusion is that there is an immediate response to the ingestion of food, probably depending somewhat upon the length of time that the animals were occupied in eating the relatively small amounts consumed. After the initial response, these small amounts of feed did not further stimulate the metabolism.

The Metabolic Stimulus of Feeding-stuffs

The metabolism of the organism is stimulated or raised above the basal requirements by the processes of digestion and utilization of food much as the fire in a furnace would flare up when fanned by a blower. The separate evaluation of the economic cost of such overhead processes with each feeding-stuff is the critical feature in the determination of the so-called "net energy values" of feeding-stuffs. The attempt to determine this economic cost by measuring the metabolism at two different feed-levels has, we believe, resulted in the utilization of an unduly low figure for the metabolism following the lower food-level. This experimental plan calls for prolonged feeding on the curtailed ration prior to the measurement of the metabolism, in order to secure uniformity of contents in the intestinal tract and hence uniformity in the determination of the digestion coefficients. By this procedure the animal is brought to a lower metabolic plane by the dual effect of the actual reduction in feed and the condition of undernutrition at least begun during the 3 weeks' period of submaintenance feeding. On the other hand, if the metabolism of an animal is first determined while he is on maintenance feed and then shortly thereafter at essentially the fasting stage, the difference between these two levels should indicate the increased metabolism of the organism due to the ingestion of food. This method is certainly justifiable when animals are fed a maintenance ration. In order to compare the metabolism on maintenance and submaintenance rations, or on a ration 50 per cent below maintenance, as was the case in our research, in all probability the curtailment should not take place more than at the most one or two days before the actual experiment, as otherwise one will be running into the dangers of incipient undernutrition with its well-known depressing effect upon metabolism.

Experiments on this special point have not yet been made, although they are in our experimental plan. If we examine the data for the 4-day experiments with steers E and F (see Table 53, p. 195) and confine ourselves to those experiments in which maintenance feeding with 7 kg. of either timothy or alfalfa hay is involved, and eliminate any experiments with unduly low chamber temperatures, we may obtain some evidence regarding the increase in metabolism due to the feed. It will be recalled that in these experiments the animal was fed 7 kg. of hay for at least two weeks prior to the experiment.

The 24-hour heat-production of steer E during maintenance feeding on timothy hay was reasonably constant at 11.6 therms[a] on December 12 to 14. In the experiment beginning 32 hours after the withholding of this ration, i. e., during the stage of so-called "fasting katabolism," the heat-production was 7.7 therms or 3.9 therms lower. Reversing the argument, one can state that a fasting katabolism of 7.7 therms was raised 3.9 therms by the regular ingestion of 7 kg. of timothy hay. In other words, there was an increase in metabolism of 51 per cent. Similarly, in the experiment from February 27 to March 3[b] the initial metabolism with 7 kg. of timothy hay was 11.1 therms. In the basal experiment beginning 32 hours after the last food it was 7.8 therms, or 3.3 therms lower. There was, therefore, in this case an increase of 42 per cent with the ingestion of 7 kg. of timothy hay. With alfalfa hay the heat-production in the March experiment was 11.5 therms during the two days on feed and 7.0 therms in the period beginning 32 hours after the last food. The increase due to the hay was therefore 4.5 therms or 64 per cent. The experiment of April 14 to 17 shows a heat-production during full feeding with alfalfa hay of 11.5 therms and 32 hours after the last food 6.7 therms, i. e., an increase of 4.8 therms or 72 per cent.

With steer F in the December experiment with timothy hay, the heat-production was 11.9 therms on full feed and 32 hours after food it was 8.1 therms. The increase due to the hay was thus 3.8 therms or 47 per cent. On March 23 to 25 the two days of feeding with alfalfa hay resulted in a metabolism of 12.5 therms, which fell to 7.7 therms on the second day without food. The difference was 4.8 therms or 62 per cent. In a second experiment with alfalfa hay in April, the heat-production on full feed was 12.3 therms and 32 hours after food was 7.5 therms. The increase was 4.8 therms or 64 per cent.

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[a] We use the Armsby term here, since in practical feeding problems it apparently has distinct advantage over the large numeral calories. One therm is equivalent to 1,000 large calories.

[b] The low environmental temperature obtaining in this experiment is seemingly without effect.

Thus with both animals it is clear that the increase in metabolism produced by the 7 kg. of timothy hay was not far from 50 per cent, but that the increase produced by 7 kg. of alfalfa hay was nearer 60 per cent. On this basis, therefore, the so-called "specific dynamic action," or preferably the "metabolic stimulus," of alfalfa hay is measurably higher than that of timothy hay. On the other hand, as has been pointed out before this, the basal heat-production with alfalfa hay, determined 32 to 56 hours after food, is perceptibly lower in general than with timothy hay. This may possibly be accounted for by the fact that the alfalfa experiments were at the end of the series with both animals. In other words, the steers had been undergoing a fairly rapid series of 2-day fasts and undoubtedly their nutritive condition must have been at a somewhat lower level at the end of the series than it was at the beginning, in spite of the mild attempts to make up for the loss between experiments. To make the study perfectly clear, the experimental series should likewise have been carried out in the reverse order. But, as stated frequently, our main object was not to study the relative merits of alfalfa and timothy hay.

These feeds are both characterized, as is most roughage for animals, by a low digestibility, that is, they are approximately 50 per cent digestible. The alfalfa hay is richer in protein than is the timothy hay, which is relatively protein-poor. Judging from experiments on men and dogs, the normal increase in metabolism due to the ingestion of food is by no means of the same order of magnitude as observed with these ruminants. Thus, Benedict and Carpenter[a] found in three 8-hour experiments, when the subject ate enormous amounts of food at one meal (the fuel value of which averaged 4,000 calories), that the total increment in heat noted in the subsequent 8 hours was 186, 229, and 148 calories, respectively. On the average the increase was 23 calories per hour. Since the heat-production was about 70 calories per hour when these subjects were resting, it can be seen that during these eight hours, when the digestive activity was greatest there was an increase of only about 30 per cent in the heat-production due to these enormously heavy meals. When referred to the actual fuel value of the meal itself, this increase (termed by the authors the "cost of digestion") is found to be not far from 5 per cent. The picture is entirely different with steers, for the ingestion of 7 kg. of hay, of which one-half only is digestible, produced not during the height of digestion but throughout an entire 24-hour period an increase in the total heat-production of 50 per cent in the case of timothy hay and 60 per cent in the case of alfalfa hay. In the case of the men the protein in the meal accounted in appreciable part for the increase, as the so-called "specific dynamic action" of protein is most marked. Timothy hay, however, contains little protein, and the stimulating effects of foods are on an entirely different plane with ruminants than with a human being. These large increases, we believe, may be easily accounted for by the nature of the cleavages which carbohydrate material undergoes in its passage through the intestinal tract. Indeed, the early suggestion of Grouven, that carbohydrates for the large

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[a] Benedict and Carpenter, Carnegie Inst. Wash. Pub. No. 261, 1918, Table 249, p. 337.

TABLE 55.—*Standard metabolism of steer C at different levels of nutrition*

Feed-level, and dates	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours			Activity
								Total	Per 500 kg.	Per sq. m.	
Realimentation; 4 to 8 kg. hay, 2 kg. meal:[1]	*kg.*		*kg.*	*°C.*	*°C.*	*gm.*		*cal.*	*cal.*	*cal.*	
Dec. 17, 1921....	558.4	40	4.8	21	21.3	56.7	(0.82)	8,100	7,300	1,440	II
Dec. 22, 1921....	570.0	38	2.2	7	11.3	59.9	(.82)	8,600	7,500	1,510	II
Jan. 23, 1922....	567.6	40	6.4	12	20.3	79.3	(.82)	11,400	10,000	2,000	II
Jan. 30, 1922....	572.2	40	......	24	21.6	81.0	(.82)	11,600	10,100	2,030	III
Maintenance; 9 kg. hay:[2]											
Mar. 21, 1922....	596.0	[3] 60	......	......	24.9	71.6	(.82)	10,300	8,600	1,750	II
Mar. 31, 1922....	592.2	40	7.4	20	22.7	66.4	(.82)	9,500	8,000	1,630	II
Realimentation; 8 kg. hay:											
May 9, 1922....	562.2	34	5.2	18	19.4	66.1	(.82)	9,500	8,400	1,680	II
Maintenance; 9 kg. hay, 2 kg. meal:[2]											
Dec. 13, 1922....	674.8	40	9.0	18	22.1	51.5	.79	7,600	5,600	1,200	II
Dec. 18, 1922....	670.8	40	12.8	26	27.0	69.4	.78	10,400	7,800	1,650	II
Dec. 21, 1922....	663.0	40	9.4	22	13.4	75.4	.84	10,600	8,000	1,690	II
Dec. 26, 1922....	674.2	40	11.2	26	26.6	66.3	.86	9,200	6,800	1,450	I
Dec. 29, 1922....	676.2	38	6.6	15	6.4	70.2	.84	9,900	7,300	1,560	II
Jan. 16, 1923[4]...	689.2	40	11.8	29	27.8	64.0	.85	8,900	6,500	1,390	III
Maintenance; 9 kg. hay:[5]											
Apr. 3, 1923....	705.6	[6] 32	9.6	21	23.1	67.5	.89	9,100	6,400	1,400	III
Apr. 11, 1923....	705.8	37	6.4	14	17.9	68.9	.83	9,800	6,900	1,500	II
Apr. 18, 1923....	704.2	[6] 38	8.2	18	22.1	69.7	.73	11,000	7,800	1,690	II
Apr. 24, 1923....	700.8	[9] 32	6.0	12	16.5	71.4	.78	10,700	7,600	1,650	I
Submaintenance; 4.5 kg. hay:[7]											
May 5, 1923....	669.0	36	7.2	22	25.5	55.7	.72	8,900	6,700	1,410	III
May 11, 1923....	664.2	38	4.4	16	20.5	65.1	.79	9,600	7,200	1,530	III
May 18, 1923....	662.2	32	5.2	18	21.5	54.8	.77	8,300	6,300	1,330	III
May 24, 1924....	655.2	32	4.4	17	23.5	56.1	.76	8,600	6,600	1,380	II
Maintenance; 8 kg. hay:[8]											
June 18, 1923....	642.8	[9] 60	7.4	20	25.9	86.3	.79	12,800	10,000	2,080	III
June 23, 1923....	649.2	[6] 46	......	23	27.4	85.5	.89	11,500	8,900	1,860	II
Maintenance; 9 kg. hay:[2]											
Nov. 28, 1923....	(690.6)	44	......	10	22.3	72.8	.87	10,000	7,200	1,550	II
Dec. 6, 1923....	690.6	40	......	13	20.3	76.9	.91	10,200	7,400	1,580	II
Dec. 13, 1923....	690.6	36	......	ca. 9	23.2	77.3	.94	10,000	7,200	1,550	II
Dec. 20, 1923....	693.2	38	......	3	19.5	57.2	.90	7,600	5,500	1,180	II
Submaintenance; 4.5 kg. hay:[2]											
Jan. 3, 1924....	(650.0)	38	......	3	14.0	60.4	.81	8,800	6,800	1,420	II
Jan. 11, 1924....	650.4	36	......	7	10.1	51.1	.83	7,300	5,600	1,180	I
Jan. 18, 1924....	655.0	36	......	7	11.9	55.6	.82	8,000	6,100	1,290	I
Jan. 24, 1924....	655.4	36	......	1	9.0	59.1	.80	8,700	6,600	1,400	II
Jan. 31, 1924....	646.4	38	......	......	14.5	56.4	.79	8,400	6,500	1,360	II
Feb. 7, 1924....	629.2	34	......	ca. 1	9.3	52.5	.80	7,700	6,100	1,270	II
Feb. 25, 1924....	631.4	34	......	1	13.8	53.4	.84	7,500	5,900	1,230	I
Maintenance; 7 kg. hay:[10]											
Nov. 26, 1924....	744.6	[11] 44	......	......	18.8	73.0	.85	10,200	6,800	1,510	I

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[1] No meal given before experiments of Dec. 17 and Dec. 22.

[2] Steer had received this feed daily for at least 2 weeks preceding the experimental series.

[3] Steer was eating.

[4] This experiment was preceded by a 3-day fast on Jan. 3 to 6.

[5] The first experiment in this series was preceded by 5 days on 9 kg. hay; before that 9 kg. hay and 2 kg. meal were given daily.

[6] Steer was lying down.

[7] The first experiment in this series was preceded by 9 days on 4.5 kg. hay; before that 9 kg. hay were given daily.

[8] The first experiment in this series was preceded by 9 days on about 8 kg. hay; for 3 days before that 3 to 6 kg. hay and 1 to 2 kg. meal were given daily.

[9] Steer had just stood up.

[10] The experiment of Nov. 26, 1924, was preceded by 4 days on 7 kg. hay daily; before that 8 kg. hay were given daily and 2 to 8 kg. meal on some days.

[11] Heart-rate on Nov. 25.

TABLE 56.—*Standard metabolism of steer D at different levels of nutrition*

Feed-level, and dates	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours			Activity
								Total	Per 500 kg.	Per sq. m.	
Realimentation; 3 to 8 kg. hay, 2 kg. meal:[1]	*kg.*		*kg.*	°*C.*	°*C.*	*gm.*		*cal.*	*cal.*	*cal.*	
Dec. 17, 1921....	584.4	40	6.8	21	22.3	59.7	(0.82)	8,600	7,400	1,490	II
Dec. 22, 1921....	590.6	40	3.6	7	17.2	58.2	(.82)	8,400	7,100	1,440	II
Jan. 23, 1922....	590.6	[2] 40	6.2	12	23.6	67.3	(.82)	9,700	8,200	1,700	II
Jan. 31, 1922....	600.2	48	......	22	21.0	81.5	(.82)	11,700	9,700	1,990	III
Maintenance; 9 kg. hay:[3]											
Mar. 21, 1922....	611.2	[4] 56	......	......	24.9	86.3	(.82)	12,400	10,100	2,080	II
Mar. 31, 1922....	612.6	40	6.8	20	22.8	73.7	(.82)	10,600	8,700	1,780	II
Realimentation; 4 to 9 kg. hay:											
May 9, 1922....	570.8	46	5.6	18	22.4	73.9	(.82)	10,600	9,300	1,860	II
Maintenance; 9 kg. hay, 2 kg. meal:[3]											
Dec. 15, 1922....	675.6	44	13.0	27	26.0	69.8	.73	11,000	8,100	1,740	II
Dec. 19, 1922....	670.8	40	11.8	23	10.5	80.2	.84	11,300	8,400	1,790	II
Dec. 30, 1922....	677.2	46	17.6	13	8.2	76.3	.82	11,000	8,100	1,730	I
Jan. 3, 1923....	676.0	48	6.2	11	8.4	76.8	.82	11,000	8,100	1,730	I
Maintenance; 9 kg. hay:[5]											
Apr. 4, 1923....	697.8	[6] 46	6.6	18	21.8	80.7	.78	12,100	8,700	1,870	III
Apr. 12, 1923....	699.2	[2] 46	7.8	14	18.9	78.3	.83	11,200	8,000	1,730	II
Apr. 19, 1923....	693.0	[2] 42	6.4	14	20.9	75.0	.76	11,500	8,300	1,780	II
Apr. 25, 1923....	693.0	[2] 36	9.0	20	23.6	77.3	.86	10,700	7,700	1,660	......
Submaintenance; 4.5 kg. hay:[7]											
May 4, 1923....	672.0	48	5.8	21	24.2	67.1	.72	10,700	8,000	1,690	III
May 12, 1923....	659.6	[8] 60	8.2	24	26.8	66.6	.74	10,400	7,900	1,660	III
May 19, 1923....	651.2	48	5.6	21	24.8	67.1	.73	10,600	8,100	1,710	III
May 25, 1923....	649.0	48	6.2	22	27.1	68.0	.73	10,700	8,200	1,730	III
June 1, 1923....	640.8	40	7.2	19	23.6	66.3	.74	10,300	8,000	1,680	III
June 8, 1923....	633.8	48	4.2	18	21.6	68.1	.78	10,200	8,000	1,670	II
Maintenance; 9 kg. hay:[9]											
June 16, 1923....	659.0	60	9.4	18	24.6	86.4	.84	12,200	9,300	1,960	I
June 22, 1923....	660.0	48	12.2	26	28.8	82.6	.85	11,500	8,700	1,840	III
Maintenance; 9 kg. hay:[3]											
Nov. 30, 1923....	683.4	48	......	9	19.8	85.2	.86	11,800	8,600	1,850	III
Dec. 7, 1923....	673.6	52	......	13	21.6	87.4	.91	11,600	8,600	1,830	III
Dec. 14, 1923....	674.0	44	......	11	18.6	79.9	.89	10,800	8,000	1,700	III
Dec. 21, 1923....	686.8	44	......	8	18.4	79.6	.84	11,200	8,200	1,750	III
Submaintenance; 4.5 kg. hay:[3]											
Jan. 4, 1924....	653.2	36	......	5	10.6	67.3	.81	9,800	7,500	1,580	II
Jan. 12, 1924....	633.6	40	......	9	11.0	60.6	.80	8,900	7,000	1,460	I
Jan. 19, 1924....	639.6	44	......	4	10.7	69.3	.82	10,000	7,800	1,630	I
Jan. 25, 1924....	644.2	48	......	5	10.1	61.9	.78	9,300	7,200	1,510	I
Feb. 1, 1924....	627.4	42	......	5	6.3	65.8	.79	9,700	7,700	1,600	II
Feb. 8, 1924....	620.6	56	......	−6	8.9	57.6	.79	8,500	6,800	1,410	II
Feb. 26, 1924....	614.6	42	......	−2	11.1	64.8	.78	9,700	7,900	1,620	I
Maintenance; 7 kg. hay:[10]											
Nov. 26, 1924....	715.2	[11] 52	......	......	17.5	81.6	.80	12,000	8,400	1,830	I

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[1] No meal given before experiment of Dec. 17 and Dec. 22.

[2] Steer was lying down.

[3] Steer had received this feed daily for at least 2 weeks preceding the experimental series.

[4] Steer was eating.

[5] The first experiment in this series was precoded by 6 days on 9 kg. hay; before that 9 kg. hay and 2 kg. meal were given daily.

[6] Steer was ruminating.

[7] The first experiment in this series was preceded by 8 days on 4.5 kg. hay; before that 9 kg. hay were given daily.

[8] Steer had just stood up.

[9] The first experiment in this series was preceded by 7 days on 9 kg. hay; before that 4.5 kg. hay were given daily.

[10] The experiment of Nov. 26, 1924, was preceded by 4 days on 7 kg. hay; before that 8 kg. hay were given daily and 2 to 8 kg. meal on some days.

[11] Heart-rate on Nov. 25.

part pass through the fatty-acid stage of fermentation, would fall in line with the theory that the stimulation of fatty acids accounts for the increased heat-production following the ingestion of food.

It is clear that this type of experiment furnishes the basis for measuring the influence of a given amount of food upon essentially the fasting katabolism of animals. In this preliminary discussion of this feature of the experiments we have not given all the attention that should be given, perhaps, to the matter of computing the metabolism to a standard day of standing and lying, as it seemed to be a refinement hardly justified at the present stage. Further study of standard foodstuffs, with this type of experimentation, are now under investigation.

The Standard Metabolism of Steers under Different Conditions

In order to determine the metabolic plane upon which the steer was living at the time of beginning a fast and to note the rapidity of recovery after fasting, a number of standard metabolism experiments were made with each of our four animals. As outlined in our earlier study of undernutrition in steers,[a] the conditions prerequisite for the measurement of the standard metabolism are that the animal should be standing quietly and should have been without food for 24 hours. Under these conditions the standard metabolism has been measured in four half-hour periods and computed to the 24-hour basis. Numerous metabolism experiments of this type were made during the feeding-periods between the fasts, the data for which have been summarized in Tables 55, 56, and 57, for steers C, D, and E and F, respectively. The measurements secured on the first day of each of the fasts of 5 to 14 days and on the first day of each of the 2-day fasts in 1923 were also made under standard conditions, and although not included in these tables, should be taken into consideration in this discussion. (See Tables 44, 45, and 46, pp. 166, 168, and 169.)

At the start it was intended to make these measurements at a chamber temperature of not far from 20° C. Subsequently it seemed desirable to study also the influence of different environmental temperatures. A few standard metabolism experiments were accordingly made at temperatures markedly lower or higher than 20° C. In addition, in order to obtain further information regarding the influence of maintenance and submaintenance rations, a series of standard metabolism experiments were made at these two nutritive levels. It is thus possible to note whether the new findings confirm the earlier results obtained with our first groups of steers subjected to prolonged undernutrition. Since steers E and F were younger than steers C and D, it is also possible to make comparisons of the influence of age.

Factors Other than the Nutritive Level which Affect the Standard Metabolism

The comparison of the different experiments may best be made by considering the heat-production per 500 kg. of body-weight or per square meter of body-surface, although on either of these two bases there are

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 197.

wide differences in the results. In the series of standard metabolism experiments with steer C, for example, the heat-production per 500 kg. of body-weight ranges from a minimum of 5,500 to a maximum of 10,100 calories, i. e., a range of 84 per cent. Similarly, on the basis of the heat-production per square meter of body-surface, there is a difference of 76 per cent between the minimum value of 1,180 calories and the maximum value of 2,080 calories. These differences can be studied intelligently only by taking account of the various factors which affect the metabolism. Presumably, differences in body-weight are ruled out by the computation on the basis of per square meter of body-surface. Age probably does not play any great rôle in the comparison of the results obtained with steers C and D (although their experiments cover a 3-year period from December 17, 1921, to November 26, 1924), as they were 3½ years old at the start. Age does play a rôle if the data for steers E and F are compared with those for steers C and D, since steers E and F were yearlings. If steers E and F are considered alone, the factor of age does not affect the comparison, since the standard metabolism experiments with steers E and F cover a period of only 3 months. Environmental temperature undoubtedly plays a rôle, for the animals were purposely studied at different temperatures. The temperature to which the animal was exposed prior to and during the test must therefore be carefully considered.

Another factor which must not be overlooked is the variability in activity. Although the steers soon became accustomed to the respiration chamber and the experimental technique, there were certain roughly measurable differences in their activity in the stall, due to differences in individuality. As shown in our earlier publication,[a] the maximum stall activity rarely results in an increase in metabolism of more than 15 per cent on the average. There were no instances of excessive stall activity during these standard metabolism experiments, however. In accordance with our conventional method of estimating the activity from the kymograph records, we have indicated in Tables 55, 56, and 57 whether the stall activity inside the respiration chamber was I, II, or III. Activity I represents the minimum degree of movement and activity III the greatest degree, but not more than 15 per cent greater than activity I. Even activity III, however, does not involve a degree of activity sufficient to vitiate an experiment, although it is perceptibly greater than activity I. As can be seen from many of these experiments, in which the activities are different but the other factors are essentially constant, there is not a great difference in the metabolism on those days when the activity varies from I to III. A typical instance is the comparison of the experiments of December 26, 1922, and January 16, 1923, with steer C. In both experiments the feed-level and the environmental temperature were the same. Activity I prevailed during the experiment on December 26 and activity III on January 16, and yet the heat-production per square meter of body-surface was 1,450 calories in the first case and 1,390 calories in the second case. Differences in activity should not, however, be wholly disregarded.

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 209.

Level of the Standard Metabolism at the Beginning of the Different Fasts

In general, the standard metabolism of steers C and D was unusually high on the first day of the different fasts, save in the fast following submaintenance feeding. Indeed, although the extreme range in the values for the first day of fasting is not any greater than the range noted in Tables 55 and 56, actually the highest values are found with both steers at the beginning of the fasts. Thus, in Table 50, page 178, it can be seen that the highest value for steer C, 2,090 calories per square meter of body-surface on the first day of the fast in November 1922, is actually somewhat higher than the highest value, 2,080 calories, recorded in Table 55. With steer D the highest initial value in any of the long fasts is 2,490 calories on the first day of the fast in November 1923, and the highest value recorded in Table 56 is 2,080 calories. These high values at the beginning of the fasts are in part to be explained on the ground that an effort was made, although perhaps only partly successful, to bring these animals by feeding to a somewhat higher nutritive plane, i. e., to at least maintenance, if not above, preparatory to withstanding the fast. This effort is undoubtedly reflected in general in these somewhat higher values noted on the first day of fasting.

Influence of Environmental Temperature Upon Standard Metabolism

In certain of these standard metabolism experiments the variation in temperature was such as to make comparisons of the influence of the different temperatures justifiable, for the other factors were held sufficiently constant to consider that the temperature factor may be the determining cause of any change noted in the metabolism. The temperature effect alone will therefore be considered at this point. With steer C on December 29, 1922, at a chamber temperature of 6.4° C. the metabolism per square meter of body-surface was 1,560 calories per 24 hours. The day before the temperature was 26.6° C. and the metabolism was 1,450 calories. On January 16, 1923, the temperature was 27.8° C. and the metabolism was 1,390 calories. Thus, seemingly the lower temperature has increased the metabolism slightly, the increase being about 100 calories per square meter of body-surface with a lowering in temperature of about 20° C. With steer D on December 15, 1922, at a chamber temperature of 26° C. the heat-production was 1,740 calories per square meter of body-surface, and on December 30, 1922, at a chamber temperature of 8.2° C. it was 1,730 calories, or practically identical with the value obtained at the higher temperature.

In this study it is of interest to compare the series of submaintenance experiments with steer D from January 4 to February 26, 1924, with the submaintenance series from May 4 to June 8, 1923. The body-weight was about the same in both cases. The environmental temperature was much higher in the spring series than in the winter series. The ration was exactly the same, but the stall activity was in general a little higher in the spring. The heat-production per square meter of body-surface is perceptibly higher in the spring series, i. e., about 1,690 calories as compared with 1,540 calories in the winter series. The average chamber temperature was about 24° C. in the spring and about 10° C. in the winter. A similar comparison of the data for steer C shows the same effect, although it is a little less striking.

This evidence tends to support our earlier suggestion made in connection with the undernutrition studies,[a] that the lower environmental temperature frequently may be accompanied by a lower heat-production. There are two contaminating features in this evidence, however. In the first place, the activity with both animals was slightly higher in the spring series, although, judging from our kymograph records of the activity of the animals when inside the respiration chamber, it would seem as if the difference in the heat-production due to a difference in activity could hardly be more than 15 per cent. If one reduced by 15 per cent the average value noted in the spring series, the average heat-production would be 1,440 calories as compared with the average value of 1,540 calories noted in the winter series of 1924. On this basis the lower temperature is accompanied by a higher and not by a lower metabolism. This is a finding fully in line with the conclusion drawn from the analysis of the data obtained in the 4-day respiration experiments with steers E and F when on submaintenance rations (see p. 200). It should be pointed out, however, that the study of the influence of environmental temperature made during the 4-day respiration experiments of steers E and F is based upon data obtained during one season only of the year and that the study of the influence of environmental temperature in the experiments in the spring of 1923 and the winter of 1924 involves the possible effect of changes in season upon the metabolism. This factor has not as yet been thoroughly studied. If we disregard for the moment, however, any possible seasonal variation in metabolism, the correction of the heat-production in the spring series of 1923 for the difference in activity brings out the fact that an average difference in temperature of about 14° C. made but a difference of 100 calories or 7 per cent in the heat-production per square meter of body-surface. It is obvious from this particular comparison that the temperature effect is much less with these large ruminants than one finds in the reported observations on other animals, although the influence of activity and shivering has too frequently been entirely overlooked in experiments with smaller animals.

Influence of Level of Nutrition Upon the Standard Metabolism

A comparison of the standard metabolism at the maintenance and submaintenance levels of nutrition shows that with steer C the heat-production per square meter of body-surface per 24 hours was not far from 1,600 calories when he was receiving maintenance rations and that it was perceptibly lower in the two series of submaintenance experiments. This finding confirms our earlier finding on the effect of submaintenance feeding. With steer D the situation is by no means so clear. The metabolism of this animal with full maintenance rations is perceptibly higher than that of steer C, averaging more nearly 1,800 calories per square meter of body-surface. On submaintenance rations the fall in metabolism is only to about 1,700 calories in the first submaintenance series, that is, from May 4

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[a] Benedict and Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 219.

to June 8, 1923, although in the series from January 4 to February 26, 1924, the fall is much more pronounced. In general, however, the data for both animals support the general contention that submaintenance feeding lowers the metabolism perceptibly.

TABLE 57.—*Standard metabolism of steers E and F at different levels of nutrition*

Steer, feed-level, and dates	Live weight	Heart-rate per minute	Insensible loss per 24 hours	Stall temperature	Average chamber temperature	Carbon dioxide produced per half hour	Respiratory quotient	Heat produced per 24 hours			Activity
								Total	Per 500 kg.	Per sq. m.	
Steer E:											
Maintenance; 5 kg. hay; 0.68 kg. meal[1]—	*kg.*		*kg.*	°*C.*	°*C.*	*gm.*		*cal.*	*cal.*	*cal.*	
Nov. 26, 1923..	264.8	52	6.4	16	21.3	50.9	0.87	7,000	13,200	1,980	III
Dec. 3, 1923..	266.4	56	5.8	15	20.0	48.3	.84	6,800	12,800	1,920	III
Dec. 10, 1923..	268.8	44	6.6	20	23.0	45.8	.85	6,400	11,900	1,790	III
Dec. 17, 1923..	270.6	48	7.0	14	18.8	48.3	.85	6,800	12,600	1,890	III
Submaintenance; 2.5 kg. hay; 0.30 kg. meal[2]—											
Dec. 28, 1923..	260.0	36	4.6	15	15.7	35.8	.80	5,300	10,200	1,520	II
Dec. 31, 1923..	258.0	36	3.2	14	13.8	36.4	.78	5,400	10,500	1,560	II
Jan. 8, 1924..	255.2	36	2.4	15	17.2	36.2	.78	5,400	10,600	1,570	II
Jan. 14, 1924..	256.2	38	2.6	......	15.7	38.4	.77	5,800	11,300	1,680	I
Jan. 21, 1924..	253.6	44	3.6	11	8.4	45.5	.76	7,000	13,800	2,030	....
Jan. 28, 1924..	252.6	44	3.0	11	15.0	40.7	.77	6,200	12,300	1,810	I
Submaintenance; 2.5 kg. hay; 0.10 kg. meal[3]—											
Feb. 4, 1924..	251.0	38	2.4	15	17.6	38.6	.81	5,600	11,200	1,640	II
Realimentation[4]—											
Feb. 18, 1924..	237.2	[5] 52	1.2	17	15.1	34.1	.76	5,200	11,000	1,580	I
Steer F:											
Maintenance; 5 kg. hay; 0.68 kg. meal [1]—											
Nov. 27, 1923..	290.0	60	5.4	18	21.8	50.9	.85	7,100	12,200	1,900	II
Dec. 4, 1923..	293.0	44	5.4	16	20.5	52.2	.85	7,300	12,500	1,940	III
Dec. 11, 1923..	296.0	52	8.0	18	22.2	46.0	.82	6,600	11,200	1,740	III
Dec. 18, 1923..	298.0	42	4.0	10	15.1	48.2	.84	6,800	11,400	1,790	III
Submaintenance; 2.5 kg. hay; 0.30 kg. meal[2]—											
Dec. 29, 1923..	285.6	38	3.4	16	20.3	45.2	.80	6,600	11,600	1,780	II
Jan. 2, 1924..	284.8	42	3.2	12	15.6	41.5	.77	6,300	11,100	1,700	II
Jan. 9, 1924..	280.6	42	2.8	16	16.7	39.6	.79	5,900	10,500	1,610	I
Jan. 17, 1924..	279.2	42	3.4	18	22.7	46.4	.81	6,700	12,000	1,840	I
Jan. 22, 1924..	278.8	38	2.6	13	20.6	44.8	.79	6,600	12,000	1,810	I
Submaintenance; 2.5 kg. hay; 0.10 kg. meal [3]—											
Jan. 29, 1924..	276.4	36	3.2	18	21.0	46.4	.79	6,900	12,500	1,900	III
Feb. 5, 1924..	272.8	40	3.0	17	16.1	42.9	.78	6,400	11,700	1,780	II
Realimentation [6]—											
Feb. 19, 1924..	260.6	[5] 64	1.8	16	16.3	34.4	.73	5,400	10,400	1,540	I

[1] The period of maintenance feeding began on Nov. 19, 1923.

[2] The period of submaintenance feeding began on the afternoon of Dec. 17, 1923.

[3] The period of lower submaintenance feeding began on the afternoon of Jan. 28, 1924.

[4] The experiment on Feb. 18, 1924, was made 24 hours after the 5-day fast of Feb. 12 to 17. The steer had consumed 1.75 kg. hay and 500 gm. meal at the end of the fast, or 24 hours before this experiment.

[5] Steer had just stood up.

[6] The experiment on Feb. 19, 1924, was made 24 hours after the 6-day fast of Feb. 12 to 18. The steer had consumed 1.45 kg. hay and 500 gm. meal at the end of the fast, or 24 hours before this experiment.

In considering the standard metabolism of steers E and F, and particularly the influence of a marked curtailment in ration, it must be borne in mind that in the series of experiments reported in Table 57 these animals were just a little over a year old. In the series of 4-day experiments from December 1924 to May 1925, however, in which the influence of submaintenance feeding was also studied (see Table 53, p. 195), they were practically a year older, or about 2½ years old. According to the standard metabolism measurements reported in Table 57, the curtailment in ration resulted at first in a material fall in the metabolism of steer E, which persisted for the three days, December 28, December 31, and January 8. There was then a tendency for the metabolism to rise during the rest of the month. Prior to the curtailment in ration, the heat-production per square meter of body-surface was approximately 1,900 calories on the average, and during the submaintenance period it was not far from 1,700 calories, i. e., there was no appreciable change in the metabolism. Similarly with steer F, the average heat-production prior to submaintenance feeding was about 1,800 calories and during the entire submaintenance period it was not far from the same. It would appear, therefore, as if the metabolism of these young animals did not react to the submaintenance régime as in the case of the older animals, probably because a strong effort to continue growing persisted at this age.

Complications arise, however, in making strict comparisons in that the temperature factor undoubtedly enters into certain of these experiments. Thus, the high heat-production of 2,030 calories per square meter of body-surface with steer E on January 21, 1924 (see Table 57), may be in part accounted for by the fact that the chamber temperature was but 8.4° C. When these animals, E and F, were studied a year later, however, in the 4-day experiments (see Table 53, p. 195), there was an almost immediate response in the metabolism to the submaintenance feeding, in spite of the fact that prior to the respiration experiment the submaintenance ration had been fed at the most for but three weeks. Here, again, the pronounced changes in environmental temperature play somewhat of a rôle, and comparisons of the various days can be made only when the environmental temperature is taken into consideration. Yet it is clear that at the age of 2½ years these animals reacted strikingly to a 3 weeks' period of lowered food intake, in that the metabolism was distinctly depressed.

Steers C and D show an almost immediate response in metabolism to the lower feed-level. In none of the experiments with steers C, D, E, and F was the submaintenance régime carried far enough to note how long the low plateau would be held. Judging from the two submaintenance series in May 1923, and in January and February 1924, there was no disposition for the metabolism per square meter of body-surface to decrease materially in the length of time covered by these submaintenance periods.

Although the analysis of the standard metabolism of these steers is complicated by the influence of factors such as environmental temperature, the amount and character of the previous feed, and the age of the animal, the most directly comparable experiments show clearly that adult animals which have been upon full feed and are presumably in a maintenance condition, respond definitely to a submaintenance ration in that they have a persistently low metabolism. The two young animals, when 1 year old, did not react so rapidly to curtailed rations, but at the age of 2½ years the substitution of a submaintenance ration in place of the maintenance ration resulted in a distinctly lower metabolism, even when the submaintenance régime had prevailed for only three weeks.

This particular feature of the rapidity of onset of a low metabolism following submaintenance rations constitutes, we believe, the danger in attempting to estimate the fasting katabolism of steers by the method of studying the metabolism of an animal on a full maintenance ration and then on a submaintenance ration, when the submaintenance ration has been given for a period of three weeks or more. These conditions introduce not only the effect of the lowered ingestion of food, which is supposed to be studied, but the depressing effect of the submaintenance régime upon the basal or fasting katabolism.

SUMMARY

(1) Two adult steers, C and D, were subjected at varying intervals during a period of 2½ years to 7 different fasts of from 5 to 14 days in length. Two of the fasts followed pasture feeding, one a submaintenance ration of hay alone, and the rest a maintenance ration of hay and meal. The effects of intermittent fasting and of sudden and marked changes in environmental temperature were studied in a further series of fasts of 2 and 3 days' duration, at approximately weekly intervals. Two younger and smaller steers, E and F, fasted for 5 or 6 days following submaintenance feeding. The gaseous metabolism measurements in all these fasts were made in three or four consecutive half-hour periods. Subsequently each animal fasted again, and the gaseous metabolism was measured in 8-hour periods during three consecutive days. A number of continuous 4-day respiration experiments (2 days on feed and 2 days fasting) were made with steers E and F when they were about 2½ years old, in which the effects of variations in the amount and character of the ration and of high and low environmental temperatures were studied.

(2) Great irregularity in the loss in weight during fasting could be explained, as during the feed periods, by irregularity in the intake and outgo of visible matter, particularly the water intake. The magnitude of the large losses during the first few days was influenced by the pre-fasting feed-level. The losses were largest in the fasts following pasture feeding. In the fasts following maintenance feeding on hay and meal the losses were much smaller, and in those which followed submaintenance feeding they were still smaller. After the fourth day of fasting the daily losses in live weight became smaller and nearly similar, irrespective of the previous ration or the individual animal. It is concluded that two animals of the same size and age, receiving feed similar in character and amount, are fairly close physiological duplicates in respect to the loss in weight during fasting. The loss or gain in live weight *per se*, however, can not be accepted as an index of change in body-tissue without taking into consideration other factors, particularly the consumption of water and the excretion of urine and feces.

(3) The insensible perspiration from day to day was reasonably constant under the same conditions of feeding, particularly if the environmental temperature remained unchanged. Marked changes in temperature, however, were often accompanied by changes in the insensible perspiration even at the same feed-level, a large insensible loss frequently appearing with a high temperature and vice versa. The chief factor affecting the magnitude of the insensible perspiration was the amount of the ration, the loss being higher with heavy feeding than with light feeding. When the steer had been fasting for 24 hours there was usually a definite decrease in the insensible perspiration, provided the temperature remained essentially unchanged. On the second day there was a still greater decrease. After the third or fourth day the loss remained practically constant at about 3 or 4 kg. per day in the fasts following maintenance or pasture feeding

and at about 2.5 kg. in the fasts following submaintenance feeding. With the resumption of feeding the insensible perspiration increased.

(4) During fasting the water consumption was affected by changes in the environmental temperature. On some fasting days no water was taken and on other days fairly large amounts were taken. Steer C, when fasting after submaintenance feeding, drank practically no water for 9 days. In other fasts the animals refused water for periods of 3 and 4 days. In general, less water was consumed in the fasts following submaintenance or pasture feeding than in those following maintenance feeding. Water may be withheld from fasting steers without detriment, especially if the steers have previously been on reduced rations or on pasture.

(5) The daily weight of fresh feces during the feed periods was in general twice that of the ration. During fasting the fecal excretion was greatly reduced, although some feces were passed daily throughout the entire fast, irrespective of its length. On the first day there was usually a small decrease in the weight of feces. On the second day the excretion was somewhat less than half as much as on the first day, save in the fast after submaintenance feeding. After the fifth day the average excretion was about 1.5 kg. per day. The number of defecations on the first day was less in the fasts following pasture or submaintenance feeding than in those after maintenance feeding. During the 14-day fast the number of defecations and the amount of each defecation gradually decreased until about the seventh day, after which there were a large number of small defecations daily. At the beginning of the fast the feces were soft and plastic, but as the quantity decreased during the fast they became visibly firmer, being dry and pilular by the fifth day. After eight days their consistency was variable, some passages being firm and fibrous and others soft. The feces were exceedingly offensive in odor toward the end of the fast. The percentage of dry matter in feces increased in some fasts and decreased in others. A satisfactory explanation for this anomalous situation was not found. The actual weight of dry matter in feces decreased rapidly until, on the fifth day, the feces contained about 0.5 kg. of dry matter, irrespective of the previous feed-level.

(6) Smaller amounts of urine were voided during submaintenance than during maintenance or pasture feeding. The volume decreased as the fast progressed, the lower level of excretion being noted in the fasts starting at the low feed-level. The volume was seemingly independent of the environmental temperature and the water intake. A maximum individual voiding of 3,048 grams was shown by one steer on the fifth day of one of the fasts following pasture feeding· Small amounts of less than 100 grams were sometimes passed. Large changes in the content of the bladder thus seem possible, even under the restricted conditions of fasting.

(7) Extensive chemical analyses of the steers' urines were made. The effect of fasting was to change the composition of the urine from one containing a relatively low per cent of urea and significantly high amounts of hippuric acid and amino acids to one in which the nitrogen distribution on the percentage basis was similar to that in the urine of man when eliminating approximately 4 grams of nitrogen. The ammonia content

was extremely low and was not increased during fasting. The content of ketone bodies was low. This, together with the low ammonia-content, indicates a lack of acidosis during fasting. In the two larger animals the creatinine excretion was relatively constant, and, per kilogram of body-weight, was similar to that of man. Little or no creatine was excreted by the two larger animals during fasting, but the two younger and smaller animals excreted noticeable amounts.

(8) The total loss of nitrogen varied with the length of the fast and the character of the preceding ration, being notably low in the fasts after submaintenance feeding.

(9) The steers seemed to adjust themselves temperamentally to fasting even more rapidly than to a submaintenance régime. After the second day no particular irritation or craving for feed was shown. No signs of lack of vigor were exhibited, the steers appearing as strong and healthy, even on the last day of the 14-day fast, as in the early stages of fasting.

(10) The animals became more quiet and inert in their muscular exertions as the fast progressed, spending a larger proportion of the time lying down than when on feed.

(11) Rumination practically ceased after the second day, persisting longer after a dry ration than after pasture feeding·

(12) The heart-rate was lower during the periods of submaintenance feeding and seemingly more rapid at the lower environmental temperatures. Fasting resulted in an almost continuous fall in the heart-rate to a level as low as 28 or 30 beats per minute in the longest fasts.

(13) The respiration-rate during fasting was about 9 or 10 per minute.

(14) The normal rectal temperature was not far from 38.2° C. and was singularly unaffected by the feed-level, the environmental temperature, or by fasting.

(15) The skin temperature was measured only during the fasts of steers C and D following submaintenance feeding. The small amount of evidence secured suggests that neither fasting nor submaintenance feeding has a marked effect upon the skin temperature, but that environmental temperature plays a large rôle.

(16) The respiratory quotient, when the steer was receiving feed regularly, was about 1.00 or above, depending somewhat upon the character of the feed and the time elapsing after feed had been eaten. On the first day of fasting the quotient was about 0.82 or 0.83. On the second and third days it was still lower, but after the third day remained fairly constant at about 0.70, indicating that the steer was burning essentially fat.

(17) The heat-production decreased markedly during the first few days of fasting, and less markedly thereafter. Uniformity in the heat-production per square meter of body-surface appeared with steer C on about the fourth day but not until the seventh or eighth day with steer D. The metabolic level of steer D was distinctly higher than that of steer C in practically all instances, in part explained by his greater restlessness. A higher metabolism was noted with steers E and F when fasting after submaintenance feeding, indicating the higher metabolism of the younger protoplasm.

(18) The short respiration experiment of four half-hour periods, even when the animal is standing the entire time, gives a computed heat-

production not far from that found in 24-hour periods when the animal is allowed to lie or stand at will.

(19) In the 4-day respiration experiments a somewhat higher heat-production was noted with alfalfa hay than with timothy hay, when a maintenance ration was fed. The submaintenance level of metabolism was much lower than the maintenance level and, referred to body-weight or body-surface, was essentially the same with both steers, regardless of the character of the ration.

(20) The environmental temperature had practically no influence upon the metabolism when the animal was receiving a maintenance ration of timothy hay or when fasting after such a ration. At the submaintenance level of nutrition with timothy hay, however, a higher metabolism was noted with a low environmental temperature, whether the animal was receiving feed or was fasting. The effect was apparently not proportional to the difference in temperature.

(21) A difference of from 20 to 30 per cent between the metabolism in the lying and in the standing position was noted on days with feed. In some instances this difference diminished during fasting and practically disappeared after the second or third day, but in other instances it persisted even to the fourth or fifth day. The correction for this difference is not so important when the value of different feeds is being compared, as it is when an approximation of the true fasting katabolism is desired. When cattle have been fed maintenance rations, a sufficiently close approximation of the fasting katabolism can be determined in general while they are standing, about 32 hours after the last food, and if a satisfactory reduction is made for lying in the measurement thus obtained, the basal metabolism per 24 hours lying may be computed. This procedure should give a value which is suitable as a base-line in studies of the superimposed effects of various factors, provided the experiments are made shortly after this basal determination.

(22) The level in the plateau of metabolism varied with the different seasons of the year and with the quantity and character of the ration. Thus, the so-called basal metabolism, when once attained after withholding feed, was seemingly not constant with the same animal, even if he had been previously upon a maintenance ration, for a higher plateau was noted after timothy than after alfalfa hay. Submaintenance feeding, particularly with alfalfa hay, lowered the level of the fasting metabolism markedly. Since it is impossible with steers to insure complete muscular repose at any time desired and complete cessation of digestive activity (except after 4 or 5 days without food), it is debatable whether any attempt to secure the equivalent of basal conditions in man is feasible. Furthermore, it does not seem necessary in general practical problems to determine this equivalent.

(23) The probable basal energy requirement of cattle is about 1,300 calories per square meter of body-surface per 24 hours, *when the animal is lying the entire time,* save during prolonged fasting or fasting following extreme undernutrition. In two instances the heat-production on this basis of computation was 1,060 and 1,190 calories. These abnormally low values are in part explained by the influence of a sudden transition from

a cold to a warm environment. In general, however, fasting *per se*, provided the level of nutrition has not been too greatly lowered by previous undernutrition, results in a heat-production per square meter of body-surface per 24 hours much nearer 1,700 calories, *when the animal is standing.*

(24) A comparison of the actually measured fasting katabolism with that computed from the metabolism on maintenance and submaintenance rations shows that the computation method gives results too low. Since the submaintenance ration was fed for three weeks or more before its effect was measured, the metabolism was determined not only under conditions of less digestive activity due to the reduction in feed but during the initial stage of undernutrition, which has been shown to lower metabolism greatly. It is suggested that the more logical method might be to measure the metabolism during a 5-day respiration experiment, in which the first two days would represent maintenance feeding and the last three days submaintenance feeding. The third day would thus be a transitional period and the level of the metabolism on the fourth and fifth days would be that caused by the reduced ration before the effect of undernutrition was manifested.

(25) The steers were extremely slow about eating after a fast, taking hours to consume even 1 or 2 kg. of hay but consuming the grain with greater relish. The metabolism increased almost immediately after the animal was fed, the size of the increase depending somewhat upon the time occupied in eating the relatively small amounts consumed. After the initial response the metabolism was not further stimulated.

(26) The ingestion of 7 kg. of hay produced, not during the height of digestion but throughout an entire 24-hour period, an increase in the total heat-production of 50 per cent in the case of timothy hay and 60 per cent in the case of alfalfa hay.

(27) The standard metabolism was frequently lower at the lower environmental temperatures. Differences in the activity of the steers obscured the results somewhat, but it is concluded that the temperature effect is much less with these large ruminants than with other animals.

(28) When the adult animals had been upon full feed and were presumably in a maintenance condition, they responded definitely to a submaintenance ration in that they showed a persistently low metabolism. Animals a year old, however, did not react so rapidly to reduction in feed, although when they had reached the age of 2½ years a submaintenance régime of only 3 weeks also resulted in a distinctly lower metabolism.

ADDENDUM

Since this report was sent to the printer, several publications from other institutions have appeared which are of interest in this connection. These appeared too late, however, to be discussed in this monograph, and we can here only call attention to the place of publication.[a]

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[a] Forbes, Braman, Kriss, Fries, et al., Journ. Agric. Research, 1926, **33**, p. 579.
Forbes, Fries, Braman, and Kriss, Journ. Agric. Research, 1926, **33**, p. 591.
Fries, Beretning fra N. J. F.'s Kongress, Oslo, June, 1926.
Titus, Journ. Agric. Research, 1926, **33**, p. 887.

ACKNOWLEDGMENTS

The experimental work in connection with the research reported in this monograph was entirely carried out at Durham, New Hampshire, under the direction of the junior author. Most of the routine work, involving the details of handling, weighing, feeding, and watering of the animals, of taking daily records of pulse, body temperature, and other body measurements, was in the hands of Mr. A. D. Littlehale. Assisted by chemically trained students, he also carried out the preparation of rations and the sampling and weighing of feeds, feces, and urine.

The gas analyses during the second year's work of this series were made by Mrs. Lois A. Ritzman. With this exception, all the gas analyses were made by Miss Helen M. Hilton, who also had charge of the routine work connected with the operation of the respiration chamber. For their fidelity and patience we are deeply indebted.

The analyses of feed and excreta for the first four fasts were made by Mr. J. A. Gallagher, under the direction of Dr. H. R. Kraybill, chemist of the New Hampshire Experiment Station. Later all these determinations were taken over by Dr. Thorne M. Carpenter, of the Nutrition Laboratory staff, who was assisted in the details of the determinations by Messrs. P. P. Saponaro, E. L. Fox, and E. S. Mills, and Miss D. L. Tibbetts. The computations of the results of these chemical analyses were carried out by Mr. W. H. Leslie with his characteristic accuracy and thoroughness.

The editing of this report, as indeed the one preceding it, was in the capable hands of Miss Elsie A. Wilson.

SUBJECT INDEX

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