

UNIVERSITY OF MISSOURI

COLLEGE OF AGRICULTURE

AGRICULTURAL EXPERIMENT STATION

Research Bulletin 193

# GROWTH AND DEVELOPMENT

*With Special Reference to Domestic Animals*

XXXI. Influence of the Plane of Nutrition on the Utilizability of Feeding Stuffs. Review of Literature and Graphic Analyses of Published Data on the Net-Energy and Specific Dynamic Action Problems

SAMUEL BRODY and ROBERT C. PROCTER

(Publication Authorized April 28, 1933)



COLUMBIA, MISSOURI

JUNE, 1933

# Agricultural Experiment Station

**EXECUTIVE BOARD OF CURATORS.**—MERCER ARNOLD, Joplin; F. M. McDAVID, Springfield; H. J. BLANTON, Paris

**ADVISORY COUNCIL.**—THE MISSOURI STATE BOARD OF AGRICULTURE

STATION STAFF, JUNE 1933

WALTER WILLIAMS, LL. D., President

F. B. MUMFORD, M. S., D. Agr., Director

S. B. SHIRKY, A. M., Asst. to Director

MISS ELLA FAHMEIER, Secretary

## AGRICULTURAL CHEMISTRY

A. G. HOGAN, Ph.D.  
L. D. HAIG, Ph.D.  
W. S. RITCHIE, Ph.D.  
E. W. COWAN, A.M.  
ROBERT BOUCHER, JR., A.M.  
LUTHER R. RICHARDSON, Ph.D.  
U. S. ASHWORTH, A.B.

## AGRICULTURAL ECONOMICS

O. R. JOHNSON, A.M.  
BEN H. FRAME, A.M.  
F. L. THOMSEN, Ph.D.  
C. H. HAMMAR, Ph.D.

## AGRICULTURAL ENGINEERING

J. C. WOOLEY, M.S.  
MACK M. JONES, M.S.  
R. R. PARKS, A.M.  
D. D. SMITH, A.M.

## ANIMAL HUSBANDRY

E. A. TROWBRIDGE, B.S. in Agr.  
L. A. WEAVER, B.S. in Agr.  
A. G. HOGAN, Ph.D.  
F. B. MUMFORD, M.S., D. Agr.  
D. W. CHITTENDEN, A.M.  
F. F. MCKENZIE, Ph.D.\*  
J. E. COMFORT, A.M.\*  
H. C. MOFFETT, A.M.  
RALPH W. PHILLIPS, A.M.  
S. R. JOHNSON, A.M.  
C. E. TERRILL, B.S.

## BOTANY AND PATHOLOGY

W. J. ROBBINS, Ph.D.  
C. M. TUCKER, Ph.D.

## DAIRY HUSBANDRY

A. C. RAGSDALE, M.S.  
WM. H. E. REID, A.M.  
SAMUEL BRODY, Ph.D.  
C. W. TURNER, Ph.D.  
WARREN GIFFORD, A.M.†  
E. R. GARRISON, A.M.  
H. A. HERMAN, A.M.  
M. N. HALEY, B.S.  
WARREN C. HALL, A.M.  
HAROLD ALLEY, B.S.  
WILLIAM E. ECKLES, B.S.

## ENTOMOLOGY

LEONARD HASEMAN, Ph.D.  
T. E. BREKETT, A.M.

## FIELD CROPS

W. C. ETHERIDGE, Ph.D.  
C. A. HELM, A.M.\*

L. J. STADLER, Ph.D.\*  
R. T. KIRKPATRICK, A.M.  
B. M. KING, A.M.\*  
E. MARION BROWN, A.M.\*  
MISS CLARA FUHR, M.S.\*

## HOME ECONOMICS

MABEL CAMPBELL, A.M.  
JESSIE ALICE CLINE, A.M.  
ADELLA EPEL GINTER, M.S.  
SYLVIA COVER, A.M.  
HELEN BERESFORD, B.S.  
BERTHA BISBEY, Ph.D.  
JESSIE V. COLES, Ph.D.  
MINERVA V. GRACE, M.S.  
FRANCES SEEDS, M.S.  
BERTHA K. WHIPPLE, M.S.

## HORTICULTURE

T. J. TALBERT, A.M.  
A. E. MURNEEK, Ph.D.  
H. G. SWARTWOUT, A.M.  
GEO. CARL VINSON, Ph.D.

## POULTRY HUSBANDRY

H. L. KEMPSTER, M.S.  
E. M. FUNK, A.M.

## RURAL SOCIOLOGY

E. L. MORGAN, A.M.  
WALTER BURR, A.M.  
HENRY J. BURT, A.M.  
ARTHUR S. EMIG, Ph.D.

## SOILS

M. F. MILLER, M.S.A.  
H. H. KRUSEKOFF, A.M.  
W. A. ALBRECHT, Ph.D.  
HANS JENNY, Ph.D.  
L. D. BAVER, Ph.D.  
HAROLD F. RHOADES, A.M.

## VETERINARY SCIENCE

A. J. DURANT, A.M., D.V.M.  
J. W. CONNAWAY, D.V.M., M.D.  
CECIL ELDER, A.M., D.V.M.  
O. S. CRISLER, D.V.M.  
ANDREW UREN, D.V.M.  
A. M. McCAPES, D.V.M.  
HAROLD C. MCDUGGLE, A.M.

## OTHER OFFICERS

R. B. PRICE, B.L., Treasurer  
LESLIE COWAN, B.S., Sec'y of University  
A. A. JEFFREY, A.B., Agricultural Editor  
J. F. BARHAM, Photographer  
JANE FRODSHAM, Librarian

\*In cooperative service with the U. S. Department of Agriculture.

†On leave of absence.



## CONTENTS

	Page
Abstract .....	5
Introduction .....	5
Definitions .....	6
1. Net Energy .....	6
2. Specific Dynamic Action (S.D.A.) .....	6
Theories of Specific Dynamic Action (S.D.A.) .....	10
1. Voit's Theory (Also Benedict's and Grafe's theories). Lusk's support of this theory .....	10
2. Rubner's theory; the influence of growth or realimenta- tion on S.D.A.; the S.D.A. of alcohol. Lusk's change of attitude .....	10
2a. The thermodynamic and thermochemic explanations of S.D.A.; contributions of Aubel, Terroine and Bonnet, Adams .....	12
3. Zuntz's theory .....	15
3a. Borsook and Winegarden's support of the Zuntz theory.....	16
4. The mass-action theory of S.D.A. Lusk's contributions....	18
The Relations Between Food Intake, Net Energy Values, and Specific Dynamic Action .....	19
1. Forbes' Data .....	20
2. Wiegner's Equation .....	22
3. Mitchell's Contribution .....	24
4. Mollgaard's Criticisms .....	24
A Graphic Analysis of the Data by Forbes, Wiegner and Mitchell....	25
1. Average digestibility, metabolizability, and utilizabty of rations. Comparison of digestibility, etc., of cattle and rabbit feeding stuffs with human foods. ....	25
2. Changes in digestibility, metabolizability, and utilizabil- ity (net-energy) with increase in the dietary gross energy....	27
3. Changes in the several losses with increase in the dietary gross energy .....	29
4. The partition of the several losses and gains at different planes of nutrition .....	29
5. The significance of "plane of nutrition" .....	32
6. The relation between heat increment and dietary intake ....	32
7. The mathematical function relating the net-energy of a feeding stuff with the level of dietary intake .....	34
8. The influence of body size on the relation between net and gross energy .....	38
Summary and Conclusions .....	40
Bibliography .....	43

## FOREWORD

The special investigation on growth and development is a cooperative enterprise in which the departments of Animal Husbandry, Dairy Husbandry, Agricultural Chemistry, and Poultry Husbandry have each contributed a substantial part. The plans for the investigation in the beginning were inaugurated by a committee including A. C. Ragsdale, E. A. Trowbridge, H. L. Kempster, A. G. Hogan, F. B. Mumford. Samuel Brody served as Chairman of this committee and has been chiefly responsible for the execution of the plans, interpretation of results and the preparation of the publications resulting from this enterprise.

The investigation has been made possible through a grant by the Herman Frasch Foundation represented by Dr. R. W. Thatcher, who has given valuable advice from the beginning of the investigation.

F. B. MUMFORD, *Director Agricultural Experiment Station.*

# GROWTH AND DEVELOPMENT

*With Special Reference to Domestic Animals*

XXXI. Influence of the Plane of Nutrition on the Utilizability of Feeding Stuffs. Review of Literature and Graphic Analyses of Published Data on the Net-Energy and Specific Dynamic Action Problems.

SAMUEL BRODY and ROBERT C. PROCTER

**ABSTRACT.**—This bulletin is devoted largely to a graphical and mathematical analysis of data concerning the influence of the plane of nutrition on the net-energy values of feeding stuffs fed to steers and rabbits. It appears that the net-energy value of a feeding stuff,  $Q_n$ , varies with the gross energy,  $Q_g$ , intake in accordance with the equation  $Q_n = A(1 - e^{-kQ_g})$  in which  $A$  is the maximum net-energy intake,  $e$  is the base of the natural system of logarithms, and  $k$  is the relative (or if multiplied by 100, percentage) decline in the successive increment of  $Q_n$  with increasing equal increments of  $Q_g$ . This decline is due to declining digestibility, metabolizability, but principally to increasing "specific dynamic action" with increasing plane of nutrition. This equation represents this relationship for an animal of a given size. To eliminate body size as an influencing factor, the value of  $A$  in the above equation must be divided by an equalizing factor (weight, area, or weight raised to some fractional power); or the ratios of net,  $Q_n$ , to digestible energy,  $Q_d$ , are represented as functions of the planes of nutrition,  $Q_p$ , when steer and rabbit data nearly coincide according to the equation  $\frac{Q_n}{Q_d} = Ae^{-kQ_p+54}$ ; or the ratios of given net-energies to net-energy at maintenance are represented as functions of the planes of nutrition (in terms of multiples of "basal metabolism") when the rabbit and steer data coincide completely. By way of introduction to the net-energy problem, a rather detailed and critical discussion is presented on the facts and theories of the phenomena of specific dynamic action with conclusions presented in the summary at the end of this bulletin.

## INTRODUCTION

Feeders of livestock, and even students of nutrition, ordinarily assume that a pound of a given feeding stuff has a given, constant, nutritive value under all ordinary conditions of food supply. Indeed, tables of caloric values of food stuffs are commonly quoted in textbooks and elsewhere, and feeding standards are formulated on the assumption of the constancy of these values.

There is, of course, no doubt about the approximate constancy of the gross caloric values per unit of food stuff; the doubt concerns rather the constancy of the *physiologic* values of the food stuffs as derived by the animal for maintenance or productive purposes. Does an animal obtain twice as much nutriment by consuming two pounds of food than it does by consuming one pound? Or does the law of diminishing in-

crements operate in animal nutrition as it does in many other biological processes?

The purpose of this paper is to discuss, critically, some of the literature, and to present graphic analyses of published data as they relate particularly to the *physiologic* or *net energy* values of feeding stuffs in relation to the amount of feed ingested. Since the net energy derived by an animal from a given amount of food is dependent, not only on the digestibility and metabolizability of the food, but also, very largely, on its so-called specific dynamic effect, therefore, in order to obtain a proper perspective a considerable portion of this report is given to a discussion of the phenomenon of specific dynamic action.

### DEFINITIONS

1. **Net Energy.**—The *net energy* of a food is that part of it which is used in the animal economy for maintenance or productive purposes. The remainder of the food energy is lost by the animal in the feces, urine, fermentation gases, and heat of specific dynamic action.

The definition of *net energy* as formulated by Armsby is that it represents the gross energy of the ration less the excreta (feces, urine, methane) and less the energy of the specific dynamic action. The *metabolizable energy* is the gross energy less the energy of the feces, urine, and methane. The heat of the specific dynamic action, therefore, represents metabolizable energy less the net energy. Gross energy less fecal energy is taken to represent the digestible energy.

2. **Specific Dynamic Action.**—This refers to the increased heat production associated with and following feeding. It is generally known that following a heavy meal, especially if it is high in protein (meat for example) there develops a sensation of warmth. This feeling of warmth becomes especially striking, often unpleasantly so, in hot weather when there is some difficulty in heat dissipation. Feeders of live stock, and especially feeders of dairy animals, express this idea, perhaps unconsciously, by referring to some feeding stuffs as being "heating", and by saying that cows are "burned out" when over-fed with high protein feeds.

The phrase *specific dynamic action* (S. D. A.) (*spezifisch-dynamische Wirkung der Nahrungstoffe*) was coined by Rubner. Kellner, Wood and Möllgaard referred to it as *thermic energy*, because this energy can be used only for heating the animal, thus differentiating it from *dynamic energy* which may be utilized for productive purposes. Zuntz and his followers referred to it as the energy of intestinal work (*Darmparbeit, Verdauungsarbeit*). We shall refer to this phenomenon simply as S. D. A.

The S. D. A. thus represents energy wasted, except, of course, in cold weather, when it is useful in keeping the animal warm, thus sparing

its stored energy which it would otherwise burn to keep warm by *chemical heat regulation*.

Rubner's (1902, p. 347) quantitative definition of the phenomenon of S. D. A. as it refers to maintenance levels of food supply may be stated as follows: If the *postabsorptive* energy expense of maintenance of a mature, normal animal (dog) at *thermal neutrality* is 100 Calories per day, then if the animal consumes 100 Calories in the form of meat, its heat production will increase to 131 Calories for the day. This increment of 31 Calories is the S. D. A. of the 100 Calories of the ingested meat. If the animal be given 131 Calories, its heat production will increase to 137 Calories, and so on as shown in the following table (Table I), not only for protein, but also for fat and sugar diets.

TABLE I.—RELATION BETWEEN THE ENERGY IN THE FOOD AND THE HEAT PRODUCTION BY THE ANIMAL (DATA BY RUBNER ON A DOG)  
(In Calories per Day)

Trial No.	Protein Diet (Meat)		Fat Diet		Cane-Sugar Diet	
	Food Energy	Heat Production	Food Energy	Heat Production	Food Energy	Heat Production
1	0	100	0	112.7	0	100
2	100	130.9	112.7	114.3	100	106
3	130.9	137.3	114.3	114.5	106	106.4
4	137.3	139.3	114.5	114.55	106.4	106.42
5	139.3	139.9				
6	139.9	140.1				
7	140.1	140.2				

Table I shows that for a protein (lean meat) diet, energy equilibrium is not attained until the animal receives 140 Calories, that is 40 per cent above the post-absorptive level; for a fat diet, equilibrium is not attained until the animal receives 14.5% above the postabsorptive level, and for cane sugar not until it receives 6% above the postabsorptive energy metabolism.

Murlin and Lusk found lower values for the S. D. A. of fat. Thus, according to Lusk (1931), "If what we now called the *basal metabolism* of a typical animal be 100 Calories per day, and 100 Calories be administered to the animal of each of the several foodstuffs on different days, then the heat production of the animal after receiving meat protein will rise to about 130 Calories, after glucose to about 106 Calories, and after fat to about 104 Calories. These are typical average results."

The above figures apply only to a *mature* animal in a normal state of nutrition. In the case of a growing animal, or an emaciated animal which would use the protein food for growth or recovery, the S. D. A. would be less, for reasons which will be presently explained. On the

other hand, the S. D. A. would be expected to be higher at higher levels of food intake.

In the case of warm-blooded animals, the measurements must be made at *thermal neutrality*, that is at an environmental temperature which does not compel the body to produce extra heat to keep its body temperature constant; for at lower temperatures the heat of S. D. A. is utilized for keeping the animal warm, thereby sparing the body from producing extra heat for this purpose by means of *chemical regulation* and masking the S. D. A. effect. Thus, Rubner found that the feeding of 320 gm. of meat to a dog at 7°C. did not increase his heat production; but feeding 320 gm. of meat at an environmental temperature of 30°C. increased his metabolism (above the post-absorptive level) by 50 per cent. The reason that there was no apparent S. D. A. at 7°C is that at this low temperature the "basal metabolism" was higher on account of heat regulation, and the heat of S. D. A. replaced the heat of chemical regulation. This is the basis of Rubner's *compensation theory* to the effect that there is a reciprocity between heat production by chemical regulation and the extra heat production brought about through the ingestion of food.

In the cold-blooded animals, on the other hand, the S. D. A. of foods is independent of environmental temperature since, in this case, there is never chemical heat regulation, the body temperatures of cold-blooded animals being only slightly above the environmental temperature at all temperatures.

The magnitude of the S. D. A. for a given meal is determined as follows: First, the postabsorptive energy-expenditure level is determined. The animal is then fed, and measurements of heat production are continued until the original metabolic level is reached. The extra energy above the basal level represents the S. D. A. of the meal. This idea is illustrated in the lower left chart in Fig. 1. The area between the calories curve and the basal level represents the S. D. A. of the 1200 gm. of meat ingested by the dog.

If it is desired to relate the heat increment of the given meal to the nitrogen metabolism increment of the given meal, then it is, of course, also necessary to collect the urine. The extra heat (above the basal level) due to the meal is then related to the extra urinary nitrogen (represented by the area between urinary-N curve and the basal level in the lower left chart of Fig. 1) due to the meal. *All the extra* heat production due to the meal must then be related to *all the extra* urinary nitrogen excreted due to the given meal.

Since the time curve of urinary excretion of a given meal often lags behind the time curve of the S. D. A. of the same meal (compare the

urinary-N and calories curves in the middle lower chart of Fig. 1), it is, therefore, necessary to take care to continue urine collections for a sufficiently long period to make certain that the basal level of urinary nitrogen excretion has been reached.

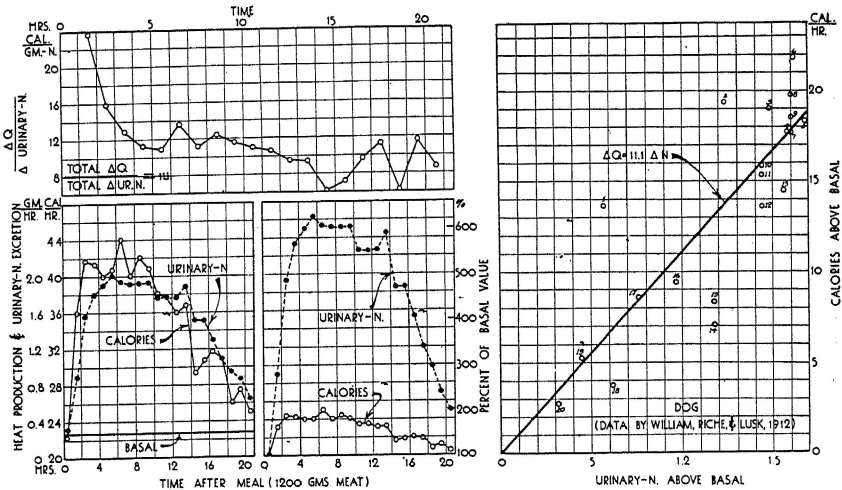


Fig. 1.—The relation between heat production and urinary-nitrogen excretion plotted from data by Williams, Riche and Lusk (1912). The data were obtained on a female bull-terrier dog weighing 13.5 kg. after feeding 1200 grams of meat and kept in a calorimeter at 26° to 27°C. The dog received no food for 24 hours preceding this feeding. The upper left chart represents the course of the ratio of Calories above basal ( $\Delta Q$ ) during given hours to nitrogen (in grams) above basal during the corresponding hours. The average ratio for the entire 21-hour period under observation is 11.1; that is, the total heat above basal produced during the 21 hours to the total urinary nitrogen excreted above basal during the same period was 11.1 Calories per gram of urinary nitrogen. (Williams, Riche, and Lusk say that "for the whole period the average increase in metabolism for every 100 calories of extra 100 calories of protein oxidized is 45 calories," and, "the ingestion of meat containing 900 calories in protein caused an increase in metabolism of 270 calories during a period of 20 hours, or the ingestion of 100 calories caused an increase of 30 calories in heat production.")

In the chart on the right, the Calories per hour above basal ( $\Delta Q$ ) are plotted against urinary nitrogen above basal ( $\Delta N$ ). The equation for this relation is given on the chart. The numerals alongside the data points indicate hours after feeding. Note that the heat production during the 1st and 2nd hour are very high in comparison to the nitrogen excretion. This is significant, but the other fluctuations are perhaps fortuitous due possibly to experimental errors (restlessness of the animal); so that the average value of the ratio of  $\Delta Q/\Delta N$  is perhaps too high. The true ratio (if the animal were absolutely quiet) is perhaps more nearly between 8 and 10 (c. f. results of Terroine, Grafe, Lundsgaard, Borsook).

The lower left chart represents the heat production and urinary-nitrogen excretion in parallel manner; in the lower middle chart the heat production and the urinary nitrogen excretion above basal are represented as percentages of the respective basal levels. This chart shows that the Calories reach a maximum value long before the nitrogen attains a maximum. It also shows that while the heat production was increased two times, the nitrogen excretion increased nearly six times. Note that the curve is not symmetrical about the maximum; the maximum occurs during the fifth hour, while the basal level is not reached again perhaps for 24-hours or longer.

Incidentally, failures to make complete urine collections due to given meals under observation invalidate much published data collected for the purpose of evaluating the S. D. A. of protein metabolism. The lowered S. D. A. in cases of certain endocrine disorders is probably apparent rather than real, being due to a slowing up of the metabolic processes with consequent oversight of the last stages of the time curves of heat production due to a given meal.

### THEORIES OF S. D. A.

How should one explain this phenomenon of S. D. A., and particularly how should one explain the quantitative differences between the S. D. A. of proteins on one hand, and of carbohydrates and fats on the other? The explanations or theories thus far advanced may be conveniently grouped under four headings as follows:

1. Voit's theory is the one most widely known and accepted in this country, largely on account of the loyal support given it by Lusk, a former pupil of Voit. According to Voit's theory, the body cells are excited by the nutrient fragments (amino acids) to a higher level of energy metabolism. Grafe's ammonia stimulating theory, and Benedict's acid-stimulating theory may, perhaps, be conveniently included in this general class.

Grafe found that ingestion of ammonium chloride and acetamide raises the heat production in the body. He attributed this to the stimulating influence of ammonia or the amino group on the metabolic level of the body cells. Lundsgaard, who has confirmed and extended these findings, believes that the cause of the S. D. A. of these substances must be sought either in some phase of urea synthesis, or, following Grafe, that it is due to the cell-stimulating action of the amino or ammonia groups liberated during deamination.

In contrast to Grafe's ammonia (or amino-radical) stimulating theory, Benedict attributes the S. D. A. to the stimulation of acid bodies, thus: "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." (Benedict and Ritzman, 1927, p. 7.)

2. According to Rubner's theory the S. D. A. of proteins represents the "free energy" liberation incident to the transformation of the excess amino acids to sugar and urea, etc. Rubner suggested a similar theory as regards the S. D. A. of non-protein foodstuffs. Thus, starch for example, may undergo some changes not only of a fermentative nature in the digestive tract, but also some intermediate metabolic changes as conversion to lactic or pyruvic acids, or it may undergo intermediate synthesis with phosphoric acid. All these (as well as certain physico-chemical incidental processes as solution and neutralization) may involve liberation of energy.

It follows as corollary from Rubner's theory that when the food amino acids are not transformed to sugar and urea, but are retained in the body as such, as, for example, during growth or during realimentation after a long fast, then there is no heat increase for the ingested proteins



thus retained. There is good substantiating evidence for this corollary by Rubner (1902, p. 256) on protein retention in dogs after starvation; by Hoobler (1915) on protein retention by infants; by Richardson and Mason on a mixed food retention administered at 2-hour intervals to emaciated diabetic patients. Lusk's comments (1931) on Richardson and Mason's experiments will be of interest to feeders of farm livestock, "We may conclude from this evidence that, if a mixed diet be so constituted as to conform to the exact needs of the tissues and be slowly introduced by absorption from the intestine, its specific dynamic action is virtually negligible, and that when there is great undernutrition the gradual digestion, absorption, and deposition of fat, added in excess of the body's requirement of energy, may be accompanied by little or no manifestation of specific dynamic action. This phase of the subject recalls the fact that the digestion, absorption, and deposition of protein is without specific dynamic action, as first shown by Rubner."

The most recent (1932) evidence was published by Necheles to the effect that the specific dynamic action of meat in Chinese children is very low compared to that found for adult Chinese and occidentals.

Another corollary may be here added that up to a certain level of protein intake the S. D. A. would be least when the biological value of the protein is greatest, and in the case of a perfectly complete protein there would be least deamination and therefore a minimum S.D.A. if fed in moderate amounts to growing animals, and the efficiency of utilization would be maximum. The opposite would necessarily be true in the case of an incomplete protein. The S. D. A. would thus be an inverse function of the degree of biological completeness of the protein under investigation when fed to growing animals up to a certain level.

It may be interesting to add in this connection that some substances can furnish to the body nothing but thermic energy (S. D. A.), and the theoretical heat value of the substances ingested may be completely recovered in the form of heat of S. D. A. Thus, grain alcohol when absorbed into the body can not be converted to glucose or fat and it is therefore of no value for maintenance or productive purposes; but since it is easily oxidized in the body it can furnish it with some heat. It is a common observation that taking of alcohol is followed by a feeling of warmth, and when taken in moderate amounts all of its potential energy can be recovered in the form of heat of S. D. A. (see Bonnet's quotation below; see also Nicloux's paper). These ideas on the S. D. A. of alcohol have not however been confirmed.

Lusk, who, as noted, loyally supported Voit's theory of cell stimulation, began to waver in later years (as indicated in the 1928 edition of the *Science of Nutrition*), and in his 1931 review of this phenomenon he

seemed to shift his position from Voit's cell-stimulating theory to Rubner's thermochemic, or thermodynamic, theory of S. D. A. of proteins.

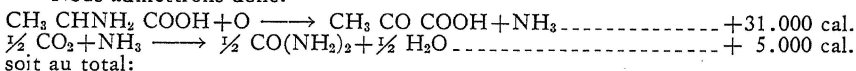
2a. Rubner experimented with meat. The very modern followers of Rubner are experimenting with well-known simple amino acids, principally with alanine and glycine, and with, what are thought to be, the intermediate products produced on the path of degradation of the amino acids.

Thus, it is assumed (as shown by Neuberg, Neubauer, Embden, and Lusk) that alanine on its course to glucose goes through the pyruvic and lactic acid stages and that (as indicated by Lusk, Aubel and others) lactic and pyruvic acids exert a S. D. A. The recent investigations in this field (by Aubel, Adams and others) then consisted in computing the energy of the reactions of alanine to glucose by way of pyruvic and lactic acids, employing in this work thermochemic or thermodynamic data and methods and attempting to confirm the computations by metabolism measurements. In this way, according to Aubel and Schaeffer (1932), "Il est possible à l'aide des données thermochemiques de calculer a chaque stade la valeur de l'action dynamique spécifique".

The latest summary of Aubel's views are given in the following fragmentary quotations from Aubel and Schaeffer (1932). In this quotation criticisms are also made against Borsook and Winegarden's theory which will be discussed presently.

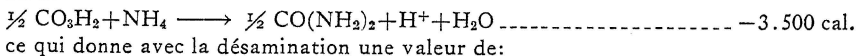
Les données que l'on possède sont insuffisantes pour permettre de calculer l'énergie libre de la réaction de désamination. Nous allons donc être forcés de nous contenter des données thermo-chimiques, mais, comme il s'agit en somme, d'un procédé d'oxydation, il est vraisemblable que les valeurs obtenues en appliquant le principe de Berthelot seront d'un ordre de grandeur comparable à celles que nous aurions obtenues si nous connaissions les entropies de l'alanine et de l'acide pyruvique.

Nous admettrons donc:



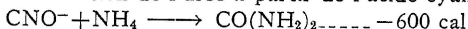
$$31.000 + 5.000 = +36.000 \text{ cal}$$

Si l'on se sert pour calculer la formation d'urée des données de Lewis et Randall, on a:



$$31.000 - 3.500 = +27.500 \text{ calories}$$

Si l'on admet la formation de l'urée à partir de l'acide cyanique:



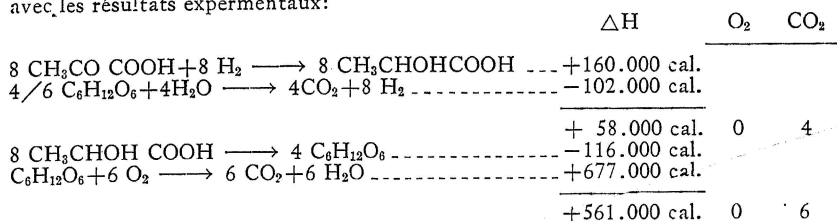
le total est alors de:

$$31.000 - 600 = +30.400 \text{ calories.}$$

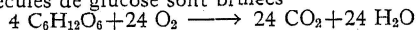
Les valeurs sont du même ordre de grandeur, et nous pouvons dire que la désamination et la formation d'urée libèrent environ 30.000 calories.

Cette valeur est tout à fait insuffisante pour expliquer l'A. D. S. dans son ensemble.

Les équations suivantes qui représentent les marches du phénomène cadrent avec les résultats expérimentaux:



Les quatre molécules de glucose sont brûlées



Si seule l'énergie de cette oxydation doit être utilisée par l'organisme, on doit ajouter à la chaleur dégagée par la combustion normale des 4 molécules de glucose formées, les chaleurs dégagées par les deux réactions précédentes:

$$58.000 + 561.000 = 619.000 \text{ cal.}$$

soit 77.375 calories par molécule d'acide pyruvique. En résumé on aurait par molécule d'alanine:

30.000 calories dues à la désamination,

77.000 calories dues à l'évolution de la chaîne carbonée soit 107.000 calories.

Aubel a trouvé chez la grenouille des chiffres qui justifient sa théorie, et, d'autre part, une confirmation indirecte est donnée par les travaux de Meyerhof, Lohmann et Meyer sur la transformation de l'acide pyruvique en glucose par le muscle isolé. D'un autre côté, Lusk sur le chien a, pour l'acide lactique, donné des résultats antérieurs à ceux d'Aubel, et également concordants. Mais Terroine, Bonnet et Zagami, n'ont pu trouver avec le lapin une production d'extra-chaleur consécutive à l'administration d'acide lactique et d'acide pyruvique.

Il reste que le schéma proposé ci-dessus, s'il rend compte de l'origine de la plus grande partie de l'extra-chaleur constituant l'A. D. S. ne doit pas rendre compte de la totalité. Il est probable que d'autres facteurs jouent et en premier lieu ceux invoqués par Krummacker, Boorsook et Winegarden; mais nous ne pouvons dire dans quelle mesure tant de nouvelles expériences irréprochables n'auront pas été faites. En ce qui concerne entre autres le rôle du travail rénal, la divergence des résultats concernant l'extra-chaleur produite par ingestion d'urée a besoin d'être levée. Les chiffres de Borsook et Winegarden, quand on les examine de près ne sont pas absolument convainquants. Les échanges sont mesurés toutes les demi-heures pendant 5 minutes, ce qui est trop court, et si l'on calcule les différences extrêmes l'on trouve, dans les témoins des variations de métabolisme de 4 cal. 3, alors que dans les expériences on a des extra-chaleurs de 5 calories, 4 cal. 6, 3 calories, 8 cal. 8. Le doute demeure.

Adams, an American worker, has computed the S. D. A. of alanine and glycine from the standpoint of the second and the third laws of thermodynamics.

It may be noted, incidentally, that Zuntz attempted to carry out thermochemic computations in 1907.

The difficulty with the thermochemic and thermodynamic computations is that (as pointed out by Borsook and Winegarden) the specific heat data at present available are too scanty to permit reliable estimations of the entropies of alanine or of glycine. Accordingly, calculations of the free energy changes incurred in the conversion of glycine to glucose and urea, although the standard free energies of glucose and urea are known, are at present uncertain. The experimental data on the S. D. A. of lactic and pyruvic acids obtained by different investigators by *in vivo* experiments are also rather too conflicting to inspire confidence in their results.

Terroine and Bonnet, who are members of another wing of Rubner's followers, differ from Aubel *et al*, as well as from Lusk school, in believing that the S. D. A. is a function of nitrogen metabolism (excretion) only, and it is independent of the structure of the amino acids. (Thus, Lusk and his pupils found that while phenylalanine, alanine, and glycine have a high S. D. A., glutamic acid, aspartic acid and asparagine give negative results.)

The following bold generalizations quoted from Bonnet (1929) summarize the theories of the Terroine School, as related to the phenomenon of S. D. A.

1.° L'action dynamique spécifique est un cas particulier d'un phénomène général: une production calorique accompagnant l'utilisation des aliments (confirmation des affirmations de Rubner).

2.° Sa valeur, chez les poïkilothermes, est indépendante de la température extérieure.

3.° Sa valeur est la même chez l'homéotherme placé à la température de neutralité thermique et chez la poïkilotherme pour toute température extérieure.

4.° Le glucose ne provoque aucune action dynamique spécifique lorsqu'il est injecté en quantité telle qu'elle ne modifie pas sensiblement le taux de la glycémie (justification de la doctrine de Rubner).

5.° L'existence d'une légère augmentation des échanges (4 p. 100) consécutive à l'ingestion de glucose, doit être attribuée à la mise en marche des différents processus digestifs; elle n'a rien de comparable à l'augmentation considérable que provoque l'administration de protides.

6.° Injecté à doses massives, allant jusqu'à quadrupler le taux de la glycémie, le glucose ne produit aucune extrachaleur.

La conception de Voit qui voit dans l'action dynamique spécifique une action excitante de masse n'est donc plus défendable.

7.° Aussi bien chez les végétaux supérieurs que chez les microorganismes, la transformation des lipides en glucides s'effectue avec une même perte d'énergie. Il en est de même pour la transformation des protides en glucides.

On peut donc formuler la loi suivante:

"Chez les êtres vivants, la transformation des lipides en glucides s'effectue avec une perte d'énergie de 23 p. 100 de l'énergie métabolisée, celle des protides en glucides avec une perte d'énergie de 35 p. 100."

8.° Cette loi nous permet de prévoir, à partir de la composition chimique des réserves d'une graine, quel sera le rendement énergétique brut dans la germination de la graine considérée.

9.° En ce qui concerne les protides, cette perte d'énergie est exactement celle que l'on observe dans le cas de l'action dynamique des protides.

Pour les lipides, elle est supérieure à celle observée dans l'action dynamique des graisses.

10.° L'action dynamique spécifique des protides, loin d'être la caractéristique d'une propriété distincte de l'organisme animal, apparaît comme un cas particulier d'une loi biochimique universelle. Elle exprime la perte d'énergie qui provient de la transformation des protides en la ou les substances utilisables pour les travaux cellulaires (glucose ou corps voisins).

11.° Le rendement énergétique brut de la croissance de moisissures, cultivées sur les divers acides aminés, est constant, très inférieur à celui obtenu dans le cas de culture sur glucose, et égal à 0, 39.

12.° La production d'extra-chaleur provoquée par l'administration de divers acides aminés, tant aux poïkilothermes qu'aux homéothermes placés à la température de neutralité thermique, est égale à 8, 4 calories per gramme d'azote ingéré.

13.° Le développement de moisissures sur les acides ternaires susceptibles de pouvoir résulter de la désamination des acides aminés, s'opère avec un rendement énergétique brut à peine inférieur à celui obtenu sur le glucose. Ce qui traduit une perte d'énergie très faible, qui ne saurait représenter le facteur primordial de l'action dynamique spécifique.

14.° Les organismes sont capables d'effectuer des remontes de potentiel peu coûteuses:

---la transformation des sucres en graisses se fait avec une perte d'énergie de l'ordre de 10%.

15.° Une réaction exothermique ne libère pas obligatoirement de l'énergie totalement utilisable par la cellule.

Il en est ainsi:

---dans la formation des glucides aux dépens des acides gras;

---dans le phénomène de désaturation des acides gras;

---dans l'utilisation de l'alcool éthylique par les homéothermes.

16.° L'action dynamique spécifique de l'alcool éthylique est égale à son énergie potentielle.

17.° Il y a deux grandes catégories d'oxydation pour les organismes: les unes (type: oxydation du glucose), libèrent de l'énergie utilisable pour tous les travaux cellulaires; les autres (type: oxydation de l'alcool éthylique) ne libèrent que de l'énergie dégradée, de la chaleur.

18.° Cultivés sur glucosamine, les microorganismes présentent un rendement énergétique brut identique à celui observé avec les différents acides aminés, soit 0,39.

19.° La loi suivante exprime en nature et en grandeur le phénomène de l'action dynamique spécifique:

"L'action dynamique spécifique des protides réside tout entière dans une production d'extra-chaleur, production qui est uniquement en rapport avec le métabolisme de l'azote aminé et non avec la transformation des chaînes ternaires résultant de la désamination, et qui s'élève à 8,4 calories par gramme d'azote aminé métabolisé."

3. According to the Zuntz theory, the S. D. A. represents the energy expense of digestion, absorption, excretion, and secretion. Zuntz grouped all these expenses under the heading of "intestinal work" (*Darmarbeit*, or *Verdaungsarbeit*). Bonnet's quotation on the S. D. A. of glucose supports Zuntz' theory that there is a certain energy expense associated with the digestion of glucose (in the sense of Zuntz). Zuntz' theory was apparently discredited by Rubner, Benedict, Lusk, and others. The experiments of these investigators consisted largely in feeding such substances as bones, glaubers salts, agar-agar, popcorn, and other roughages and irritants. They found no appreciable increase in heat production following this type of feeding, and they consequently concluded that Zuntz' theory of *Verdaungsarbeit* can not be true. But in this conclusion, they seem to have overlooked the fact that this term as used broadly by Zuntz was intended to include not only the mechanical work of peristalsis, but also the physico-chemical work of secretion, absorption, and excretion; and, of course, there is relatively little of physico-chemical work connected with the ingestion of bones, agar, or even of cathartics. In the case of farm animals, particularly ruminants, one must also consider the additional energy expense during digestion due to the extensive fermentation processes. Thus, according to Markoff, the heat production associated with  $\text{CH}_4$  formation in the digestive tract is 6.07 Calories per gram of  $\text{CH}_4$  formed; and since according to Armsby 4.5 grams of  $\text{CH}_4$  are produced per 100 grams of digested carbohydrates, therefore 27.3 Calories of heat are liberated per 100 grams of digested carbohydrates, or 7.2 Calories of heat are lost per 100 Calories of carbohydrate digested.

3a. Borsook and associates have called attention in connection with this problem to the very considerable energy expense associated with the activity of the kidneys, as determined experimentally by Barcroft and associates (1905-6), and showed (1933) that the synthesis of urea from ammonia and carbon dioxide by liver tissue is accompanied by measurable increases in oxygen consumption. These investigations give a new meaning to Zuntz' theory of S. D. A. Borsook and Winegarden's statements indicate that the energy expended for the work of secreting one gram of nitrogen by the kidneys is from 6 to 11 Calories (or on the average about 8.5 Calories per gram of urinary N.). If it is recalled that Grafe found that ammonium chloride and acetamide exert a large S. D. A.; that Terroine and Bonnet (see quotation from Bonnet) found that the ingestion of one gram of nitrogen in the form of protein or amino acids increases the heat production by 8.4 Calories; that Williams, Riche, and Lusk (1912) found a heat production of about 11 Calories per gram of urinary nitrogen (see Fig. 1); and that Lundsgaard showed that not only amino acids (glycocol, alanine, glutamic acid, aspartic acid, tyrosine) but even ammonium salts, such as ammonium chloride, increase the metabolism by about 8 Calories per gram of nitrogen ingested, then it would seem that the largest increase in heat production due to ingestion of protein must be attributed to the work of secretion, absorption, and to the excretion of the end products of nitrogen metabolism, including synthesis of urea from its precursors.

Borsook and Winegarden admit that the theoretical energy required for urinogenesis is only 0.07 Calories per gram of urinary nitrogen; but as a matter of fact, the actual energy expended by the kidney, as noted above, is about 8.5 Calories per gram of urinary nitrogen excretion; this discrepancy between observed and computed values is attributed to the low efficiency (about 1%) of the kidney, considered as a machine.

Mitchell and Hamilton (1929) cite Barcroft and Shore to the effect that the consumption of oxygen by the organs drained by the portal vein is equivalent to from 0.008 c.c. to 0.013 c.c. per gram of viscera per minute in unfed cats, and to 0.011 c.c. to 0.018 c.c. in cats fed 18 hours previously. These differences would, no doubt, be much greater if the later values were taken at the height of digestion instead of in the last stages of digestive activity. Barcroft and Piper are also cited as having found that the oxygen consumption per gram of tissue per minute of the submaxillary gland of the cat rises from a basal level of 0.027 c.c. to 0.089 c.c. when secreting. This is equivalent to the consumption of about 18 c.c. of oxygen for the formation of 30 c.c. of saliva (or about 3 Calories per liter of saliva).

Bayliss cites experiments showing that exceedingly low efficiencies are characteristic of glandular processes (e. g., six Calories are expended for the secretion of one liter of saliva). There is no reason to suppose that other such processes associated with nutrition are more efficient. In addition to secretion of urine and saliva, one thinks in this connection, for example, of the secretion of highly acid juice in the stomach, and of highly alkaline juices in the small intestines from a neutral blood.

The curves in Fig. 1 show quite convincingly that the rate of rise of heat production due to the S. D. A. is much greater in the beginning than the rise of nitrogen excretion. Indeed, the highest rise in heat production occurs during the first hour, that is probably before the nutrients entered the blood stream. This seems to substantiate the idea that the early high values of the S. D. A. represent at least in part the energy expense of the "intestinal work" in a broad sense, including the energy expense of the highly inefficient secretory processes.

These considerations taken together with the findings of Williams, Riche and Lusk; of Grafe; of Terroine and Bonnet; of Lundsgaard; throw a very attractive light on the theory that the S. D. A. of proteins represents largely the work of the secretory, assimilatory, and excretory processes, and of ureagenesis.

Four recent papers need be cited in this connection even if they add confusion to this problem. First, is the report by Krebs to the effect that kidney tissue *in vitro* deaminates amino acids (to form  $\text{NH}_3$ ) far more rapidly than any other organ (the rate of formation of  $\text{NH}_3$  being as high as 0.0038 mg. per hour per mg. of dry kidney substance), and that  $\text{O}_2$  is essential for this reaction. It appears that keto acids are formed as follows:  $\text{RCH}(\text{NH}_2)\text{CO}_2\text{H} + \text{O} \longrightarrow \text{RCOCO}_2\text{H} + \text{NH}_3$ . The oxygen consumption of the kidney as determined by Barcroft and associates thus appears to be in part a consequence of this deamination reaction.

Second, is the very recent (1933) report by Borsook and Keighley to the effect that the synthesis of urea from ammonium bicarbonate in the presence of living tissue strips is accompanied by increases of oxygen consumption; and that this oxygen is used primarily to meet a stoichiometrical relation rather than supply needed energy. In a personal communication, Dr. Borsook described the matter thus:

"We have been studying the energy change in the synthesis of urea from ammonium bicarbonate by living liver pieces. The results now available make it seem quite certain that the determining factor in the total energy change in this coupled reaction is not the energy necessary, but the stoichiometrical relationships. Thus, one molecule of extra  $\text{O}_2$  is used for every mol of urea synthesized. When, as in the case when lactate is the fuel for urea synthesis, the fuel also takes part in another synthesis (i. e., the production of glycogen); then the energy of the burned lactate is shared between the urea synthesis and the glucogen synthesis. The result is that, when glycogen synthesis from lactate is in progress, the addition of another synthesis

(i. e., urea) does not increase the respiration. When there is no such additional synthesis, for every mol of urea synthesized there are about one hundred thousand calories produced by the extra respiration, where actually only seven thousand are necessary. This apparently is because the combustion of one mol of  $O_2$  is the only way in which the tissue can obtain the necessary mol  $CO_2$  in a form which can be used in the urea synthesis."

Third, is the conclusion by Doch to the effect, "that at least 80% of the S. D. A. is due to the increased energy liberated by the hepatic cells during protein ingestion" and that "The oxygen consumption of the kidney, was the same in rats on high and low protein intake, although the total oxygen intake of the former was 35% greater than of the controls on the low protein diet." Finally, one may mention Mark's curious finding to the effect that liver protein exercises an insignificant specific dynamic effect, or may even depress heat production; and that proteins from the spleen, kidney, and thymus, have reduced specific dynamic effect. Mark attributes unique heat-stimulating properties to muscle proteins.

4. In conclusion, we may cite the mass action theory of S. D. A. According to this theory, the increased concentration of given metabolites in the body accelerates the speed of their metabolism in accordance with the chemical law of mass action. Krummacker is the leading exponent of this theory. Lusk's plethora theory as it relates to fats, and to carbohydrates, belongs in this class. But recently (1931), Lusk suggested that the S. D. A. of carbohydrates may be "due to the heat of the intermediary reactions between glucose and glycogen".

The mass-law theory of S. D. A. is rather satisfactory in the light of older work as it concerns fats and carbohydrates, for the following two reasons. First, when these foodstuffs are ingested, then the heat of S. D. A. takes place at the expense of these respective nutrients as shown by the respiratory quotients (Lusk, 1912 and 1915, J. Biol. Chem., 13, 27, and 22, 15). Second, under conditions of work, the energy of S. D. A. may be used in part at least to cover the energy expense of the work (Anderson and Lusk). In other words, when the animal is called upon to expend energy at a rapid rate, then the concentration of the nutrients in the blood stream is kept at a low level, and therefore if the phenomenon of S. D. A. is an expression of the mass law, then the heat of S. D. A. tends to be depressed or to disappear. According to Carpenter and Fox (*Arbeitsphysiologie*, 1931 7, 570) the S. D. A. of fructose can not be thus used for the work while part from glucose may be so used.

In the case of work after a protein meal, on the other hand, the total heat production is the sum of the energy expended for the work, and of the S. D. A., there being no depression of, or utilization of, the heat of



S. D. A. of protein for the energy requirements of work (Anderson and Lusk); nor do the values of the respiratory quotient after a protein meal give encouragement to the mass-law explanation. It thus seems that the heat loss of S. D. A. of protein is unavoidable, being the result of some mechanism other than that of the mass law. However, as suggested by Mitchell and Hamilton (1929, p. 444) it is possible (according to the theories of Hill, Meyerhof, and associates, on the source of muscular energy) that this difference between the behavior of S. D. A. of proteins on one hand, and carbohydrates on the other hand, may be an expression of the fact that while amino acids can not be used directly for muscular work, glucose is readily used in this way.

It is probable that S. D. A. is an unknown function of many, or all, of the factors considered in the above theories; and that the true quantitative formulation of the ultimate explanation of S. D. A. will await the accumulation of adequate data on the contributions of each of the factors enumerated to the total heat of the S. D. A.

#### THE RELATION BETWEEN FOOD INTAKE, NET ENERGY VALUES, AND SPECIFIC DYNAMIC ACTION

As explained in the preceding section, food intake up to the maintenance level would not be expected to increase very greatly the S. D. A., since this would not increase greatly the work of ureagenesis or urinogenesis; nor the heat loss due to deamination; nor the concentration of metabolites in the blood. In the words of Lusk (1931), "In normal life the liver regulates the composition of the blood so as to provide fuel for the maintenance of a constant basal metabolism. If, now, the quantity of food which enters the circulation is exactly equal to the quantity needed for metabolism in the tissues, one may understand that such food merely replaces what the liver would have delivered to the blood." This principle is made use of in connection with basal metabolism determinations by permitting the subject to partake of a light breakfast before making the measurements. (Benedict and Benedict, 1923; Soderstrom, Barr, and DuBois, 1918; Wang and Hawks, 1930.)

This same line of reasoning, as explained in the preceding section, leads to the conclusion that feeding rapidly-growing or emaciated animals should not be followed by an appreciable specific dynamic action; for in such cases the amino acids will be rapidly removed from the circulation and deposited in the body tissues for growth or recovery.

This principle has not, apparently, been widely accepted by students of nutrition of farm animals; for the most extensive investigations on the S. D. A. of feeding stuffs of cattle, namely those conducted by Armsby and associates, were made on animals receiving sub-maintenance rations,

and then the results were extrapolated linearly for use on normally-fed, or super-fed, animals.

Armsby and associates were not interested in the phenomenon of S. D. A. as such, but rather in the more practical problem of evaluation of the *net energy* of feeding stuffs. We shall devote the remainder of this paper to a rather detailed discussion of three recent important contributions to this problem of net energy.

**1. Forbes' Data.**—Forbes and associates perceived the possibility of error in Armsby's assumption "that the heat increment varies directly as the dry matter; that is, that it is a linear function of the amount of feed." They have, accordingly, subjected Armsby's assumption to an experimental test. They did this by measuring heat production in steers on seven different planes of nutrition, namely, on fast, half maintenance, maintenance, one and a half maintenance, twice maintenance, two and a half maintenance, and three times maintenance. According to Forbes and Kriss (1931), the resulting curves in which the total heat production is plotted against food consumption (shown in Fig. 2) are S-shaped. Their description of the curve is as follows.

"With the heat production of the fourth day of inanition as the base value, the heat production increased slowly between fasting and maintenance, and much more rapidly above maintenance, but with a decreased rate of rise between the planes of twice and three times maintenance.

"The curve of heat production in relation to the plane of nutrition was found, therefore, to be a reversed or S curve.

"The heat production of fasting being considered as including two factors, a waste of heat utilization of body nutrients katabolized, and a theoretical minimum base value, including no such waste—the curvature of the line of heat production in relation to increasing food consumption is interpreted as resulting from. (1) The increasing concentration of metabolites circulating in the blood; (2) The change in the proportions of protein, fat, and carbohydrates katabolized, with increase in the katabolism of food nutrients and decrease in the katabolism of body nutrients; (3) the energy expense of synthesis of body nutrients (fat from carbohydrates); and (4) the decreased metabolizability of the food at the higher planes of nutrition."

No doubt can be entertained concerning the increase in slope in these curves between fast and maintenance—a fact, which, as previously explained, might be anticipated from the general theories of S. D. A.; but it is not altogether clear what significance should be attached to the *decline* in the slope of the heat curve following the twice maintenance level. It is rather difficult to conceive a good reason for such a decline *unless it be due to a corresponding decline in digestibility at the higher levels*. The following interpretation is offered by Forbes and Kriss (1932).

"The causes of the curvature of the line representing the relation of the heat production to the food consumption of cattle, with rise in the plane of nutrition from fasting to full feed, seem to be virtually as suggested in former publications (1) the increase in intermediary metabolism resulting from increasing concentration of circulating metabolites; (2) the decrement of waste heat of utilization of body nutrients, between fasting and maintenance; (3) changes in the proportions of protein, fat and

TABLE 2.—THE RELATIONS BETWEEN PLANES OF NUTRITION AND GROSS, DIGESTIBLE, ETC., ENERGY INTAKES; ALSO THE LOSSES (FECES ETC.) AT CORRESPONDING PLANES. THE PLANES OF NUTRITION ARE REPRESENTED IN TERMS OF MULTIPLES OF THE POSTABSORPTIVE HEAT PRODUCTION ("BASAL METABOLISM" OR B). PLANES 1.0B, 1.5B, AND 2.0B REPRESENT RESPECTIVELY 1.0, 1.5, AND 2.0 TIMES THE "BASAL METABOLISM," AND THE CORRESPONDING GROSS, DIGESTIBLE ETC. ENERGY INTAKES FURNISH *Net-Energy* EQUIVALENTS TO THE 1.0, 1.5, AND 2.0 TIMES THE "BASAL METABOLISM." THE NUMERICAL VALUES GIVEN IN THIS TABLE WERE INTERPOLATED CAREFULLY FROM THE CURVES OF THE SEVERAL CHARTS.

	Av. of Forbes' Four Steers—Av. Wt. =433 Kg.								Mitchell's Steer—Av. Wt. 613 Kg.								Wiegner's & Ghoneim's Rabbit SB—Av. Wt. 2.81 Kg.			
	Cal/Day				Cal/Kg/Day				Cal/Day				Cal/Kg/Day				Cal/Day		Cal/Kg/Day	
	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	0.5B	1.0B
Plane of Nutrition	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	1.5B	2.0B	0.5B	1.0B	0.5B	1.0B
Gross Energy ----	7200	15132	26700	42900	16.6	34.9	61.7	99.1	7300	17500	29700	43200	11.9	28.5	48.5	70.5	100	351	35.6	124.9
Digestible Energy	5300	11142	18900	28650	12.2	25.7	43.6	66.2	6100	14100	22350	31200	9.95	23.0	36.5	50.9	72	200	25.6	71.2
Digest. Less Methane E.	4600	9825	16800	25650	10.6	22.7	38.8	59.2	5300	12200	19600	27500	8.65	19.9	32.0	44.9	----	----	----	----
Metabolizable Energy-----	4250	9136	15750	24100	9.82	21.1	36.4	55.7	5050	11720	19000	26400	8.24	19.1	31.0	43.1	68	176	24.2	62.6
Net Energy-----	3840	7680	11520	15360	8.87	17.7	26.6	35.5	4760	9520	14280	19040	7.77	15.5	23.3	31.1	65.5	131	23.3	46.6
"Basal Metabolism"----	7680	7680	7680	7680	17.7	17.7	17.7	17.7	9520	9520	9520	9520	15.5	15.5	15.5	15.5	131	131	46.6	46.6
Feces Energy----	1900	3989	7800	14250	4.39	9.21	18.0	32.9	1200	3400	7350	12000	1.96	5.71	12.0	19.6	28	151	9.96	53.7
Methane Energy----	700	1317	2100	3000	1.62	3.04	4.85	6.93	800	1900	2750	3700	1.31	3.10	4.49	6.04	----	----	----	----
Urine Energy----	350	689	1050	1550	.81	1.59	2.42	3.58	250	480	600	1100	.41	.783	.98	1.79	10	20.5	3.56	7.3
S.D.A. Energy----	320	1460	4320	7120	.74	3.37	9.98	16.4	80	2180	4880	7580	.13	3.56	7.96	12.4	2.5	45	.89	16.4
Storage Energy----	-3840	0	+3840	+7680	-8.87	0	8.87	17.7	-4760	0	+4760	+9520	-7.77	0	7.77	15.5	-65.5	0	-23.3	0
Total Heat Production-----	8000	9140	12000	15800	18.5	21.1	27.7	36.5	9600	11700	14400	17100	15.7	19.1	23.5	27.9	133.5	176	47.5	62.6
	Gms/Day				Gms/Kg/Day				Gms/Day				Gms/Kg/Day				Gms/Day		Gms/Kg/Day	
Dry Matter Consumption-----	1650	3366	5950	9600	3.81	7.77	13.7	22.2	1650	4000	6800	9900	2.69	6.53	11.1	16.2	22	80	7.83	28.5
Nitrogen Consumption----	32	68.6	123.5	189	.07	.158	.29	.44	31	73	123	186	.05	.119	.20	.30	.47	1.64	.17	.59
Urinary-N Excretion-----	40	45.8	65	89	.09	.106	.15	.21	(30)	42	65	78	.05	.069	.11	.13	.62	.565	.22	.20
Ratio Net E./Gross E., %-----	53.3	50.8	43.1	35.8	----	----	----	----	65.2	54.4	48.1	44.1	----	----	----	----	65.5	37.3	----	----

carbohydrates katabolized, and probable (but unestablished) differences in the specific dynamic effects of these different katabolized nutrients; (4) the energy expense of synthesis of fat from carbohydrate, above maintenance; (5) the decreasing metabolizability of food at the higher planes of nutrition; (6) the heat of fermentation of carbohydrate nutrient; and (7) the physical work of food utilization."

Whatever one may think of Forbes interpretations, there is no doubt that the numerical data by this group of workers constitutes an exceedingly important contribution to the net-energy problem.

2. **Wiegner's Equation.**—A similar investigation by Wiegner and Ghoneim (1930) on a rabbit appears to substantiate in most respects the results of Forbes and associates, although Wiegner's results are presented in a different form so that it is difficult for the reader to perceive the similarity between Forbes' original curves, and the curves of Wiegner. For the sake of convenience, Wiegner's curves are reproduced alongside Forbes' curves in Fig. 2.

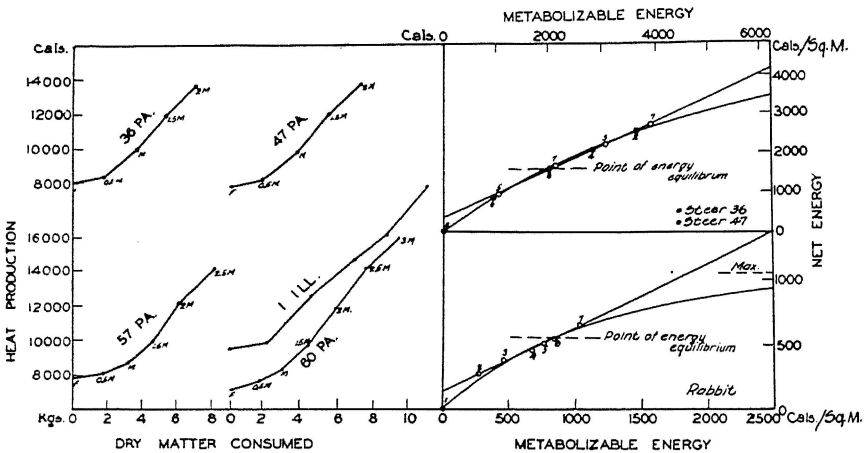


Fig. 2.—The curves in the left chart, representing heat productions as functions of dry matter consumed, were traced from Forbes *et al* (labelled Pa.), and from Mitchell *et al* (labelled Ill.). Note the S-shaped form, and the decline in slope in the last segment of the Pa. curves, and the absence of such decline in the Ill. curve. The curves in the right chart, representing the net energy of the food consumed per unit surface area as function of the corresponding metabolizable energy, were traced from Wiegner and Ghoneim. The curves here represent the equation proposed by Wiegner and Ghoneim, while the straight line represents a linear relation as would have presumably been used by Kellner, Armsby and others in connection with these data.

Fig. 2 shows that while Forbes plotted total heat production against total dry matter consumed, Wiegner presented his results in the form of net energy per unit area per day as a function of metabolizable energy per unit area per day. While Forbes presented empirical data, Wiegner was more interested in formulating a quantitative theory of energy utilization.

Wiegner's theory is, in brief, that the net energy of a feeding stuff does not vary linearly with the food ingested (as was generally assumed, until the appearance of the paper by Forbes *et al*), but that the successive

increments of net energy decline with successive increments of food consumption in accordance with the equation

$$\frac{dA}{dF} = K(H - A) \quad (1)$$

in which  $A$  is the net energy of the feeding stuff (Kalorien der Nettoenergie des Futters);  $F$  is the metabolizable energy of the feed (Kalorien des Physiologischen Nutzwert des Futters);  $H$  is the maximum net energy of the feed (Hochstzale der Kalorien der Nettoenergie des Futters);  $K$  is the efficiency coefficient (Wirkungskoeffizient unabhängig von Ernährungsniveau).

Equation (1) is then presented in the integrated form

$$\ln \frac{H}{H - A} = KF \quad (2)$$

which is the equation of Wiegner's curves in Fig. 2.

It may be noted, quite incidentally, that the ideas of Wiegner are based on the "law of diminishing increments"; also that equations (1) and (2) represent the well-known "law of mass action" formulated and proposed by Wilhelmy in 1850 to represent the fact that the velocities of chemical reactions at any moment are, in the case of reactions of the first order, proportional to the concentrations of the reacting substances.

As regards the relation between available plant nutrients and plant growth this "law" was first proposed by Liebig and formulated mathematically by Mitscherlich. Spillman and more recently Jull, Titus, and Hendricks, and Hendricks, Jull and Titus have extended this idea by relating food consumption to the amount of growth in animals. Hendricks wrote the differential equation of this relation in the form of

$$\frac{dW}{dF} = K(A - W) \quad (1a)$$

indicating that the gain in live-weight per unit of feed intake is directly proportional to the difference between some constant,  $A$ , and the live weight already attained,  $W$ . It is clear that equations (1) and (1a) are similar. The integrated form is written by Hendricks in the form of

$$W = A - Be^{-kF} \quad (2a)$$

which is similar to equation (2).

We have previously used (e. g., Mo. Res. Bull. 97) equations of the form of (1a) and (2a) above to represent the course of growth with increasing age ( $t$ , age, was used in our equation in place of  $F$ , food consumption). These historic remarks concerning the mass-law (or diminishing-increment law) equation are made by way of emphasis on the wide applicability and general usefulness of the exponential equation

for representing relationships in biochemical and physiological processes, as well as in physical and chemical processes. The idea of relating net energy to food intake with the aid of this useful equation is evidently a very helpful contribution. These authors, as already indicated, also contributed data on the net energy values of feeding stuffs in the rabbit.

**3. Mitchell's Contributions.**—Mitchell and associates published (1932) data similar to those by Forbes and associates, but confining the work to one particularly suitable steer which was larger (weight 613 kg.) than Forbes' steers (average weight 433 kgs.). The curve labeled "1 Ill." in Fig. 2 represents Mitchell's steer. The total heat production of Mitchell's steer for given dry matter intake shown in Fig. 2 is, of course, higher for Mitchell's than for Forbes' steers since Mitchell's steer is much larger.

As previously noted, Forbes *et al* found a downward trend in the heat production curve represented in Fig. 2; Mitchell *et al* on the other hand do not find such a decline, and express the opinion concerning Forbes' data that "the significance of the downward trend at the higher levels of nutrition may be questioned both because they are in all cases slight and because they occur at different levels of feeding when noticeable at all." The present writers agree with Mitchell in this criticism as far as it concerns the downward trend at the higher levels. Mitchell and associates differ from Forbes and Wiegner in concluding that, "except for submaintenance levels of feeding, the net energy bears a linear relation to the amount of dry matter consumed."

Mitchell and associates emphasize that "the lowest level of feeding was associated with the most complete digestibility of all nutrients" and that "there was a progressive decrease in digestibility from the lowest to the highest ration only in the case of nitrogen-free extract, ether extract, and dry substance."

**4. Möllgaard's Criticisms.**—Before closing, it is necessary to call attention to Möllgaard's monograph (1929) in which he shows that the net energy of a given feeding stuff depends primarily upon its use (maintenance, fattening, milk production, work) and on its composition (e. g., protein level). After the appearance of Forbes' and Wiegner's papers, Möllgaard (1931) criticized them on grounds of poor technique, faulty methods of computations, general inconsistency of results, and faulty generalizations. Some of these criticisms are presumably applicable to Mitchell's paper. There is no doubt that criticisms by one of Möllgaard's experience and ability must be considered very seriously. We shall not, however, enter into the details of the criticisms, and the reply thus elicited from Wiegner, because, frankly, we are not competent to do this. In the following discussion, we shall tentatively assume the correctness of the data by Forbes, Wiegner, Mitchell, and their associates. Any defects, if present, will come to the surface sooner or later.

## A GRAPHIC ANALYSIS OF THE DATA BY FORBES, WIEGNER, AND MITCHELL

1. Average Digestibility, Metabolizability and Utilizability of Rations.—It is clear from the preceding discussion that the digestibility, or metabolizability, or utilizability (net energy) of a ration depends on the plane of nutrition, and it is not possible to represent any of these by constants; or, in the words of Mitchell, *et al.*, "The net energy value of a ration may be defined not by a constant, as Armsby supposed, but by an equation relating it to the intake of dry matter." Nevertheless, it seems desirable for purposes of simplification to have before us constants, that is average values, for digestibility, metabolizability, and utilizability (net energy). These are presented in Fig. 3, based on the data by Forbes and Mitchell for the steer, and by Wiegner for the rabbit. The chart on the right of Fig. 3 represents coefficients of digestibility; the chart on the left represents digestible energy, metabolizable energy, and net-energy respectively as percentages of gross energy intake.

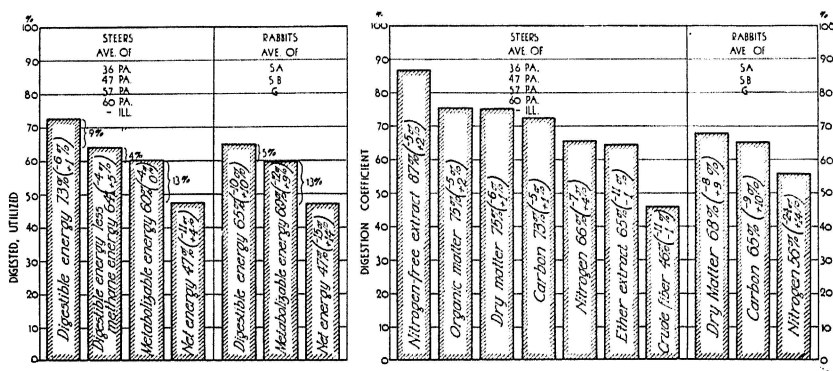


Fig. 3.—Average digestibility, etc., of the rations used by Forbes and Mitchell for steers, and by Wiegner and Ghoneim for rabbits. See text for detailed explanations.

In Fig. 3, the height of the columns and the average figures there given, represent the averages of *all* data for *all* steers (Forbes' 4 steers, labelled "Pa.", and Mitchell's one steer, labelled "Ill."). The rabbit columns likewise represent the averages of *all* experiments in the SA, SB, and G series. The average numerical values in the columns are followed by minus or plus sign values in parentheses. The upper numbers in the parentheses must be deducted from the averages to obtain the value gotten by Forbes for steer 60 on the highest plane of nutrition. Thus, the average digestible energy of all steers is 73% of the average gross

energy intake of all steers; but the digestible energy of steer 60 on the three times maintenance ration (the highest plane) is  $73-6=67\%$  of the gross energy intake. Steer 60 on the 3M plane was chosen for this purpose because this steer on this ration gave the lowest values for digestibility, etc. The lower numerals in the parentheses indicate the amount that must be added to the average value in order to obtain the *average* digestibility, etc., of the 4 Forbes' steers on the *maintenance* ration (at which plane digestibility, etc., was at a maximum), (except for net energy which is a maximum at  $\frac{1}{2}$  M for all steers except No. 60 "Pa."). Thus, the average digestibility of the ration by Forbes' 4 steers on 1-maintenance is  $(73+1)\%$  of the gross energy intake. In the case of the rabbit, the upper value must be deducted to obtain the *average* digestibility, etc., on the highest plane; and the lower value must be added to obtain the average digestibility, etc., on the lowest plane.

It is interesting to note that while the average digestibility in the rabbit is somewhat below the average in the steer, the averages of the metabolizability and utilizability (net-energy) of the rations are the same in both species; but it must be remembered that Wiegner had one or two data points above the maintenance level while Forbes and Mitchell had several points above maintenance. It is probable, however, that for practical purposes the rabbit might serve very well as an experimental animal for evaluating metabolizable and net energies of cattle feeds.

It is evident that the digestibility and metabolizability of the cattle and rabbit feeding stuffs are much inferior in these species than are human foods in the case of humans. Thus, Sherman (1932, p. 140) quotes the *physiological fuel values* (which correspond to our metabolizable values) to be 4 Calories per gram of each, carbohydrates and proteins, and 9 Calories per gram of fat. These values were obtained on the assumption that the digestibilities are 92% for protein, 95% for fats and 98% for carbohydrates. Sherman also assumes that the digestibility and metabolizability of carbohydrates and fats are the same; that is, that there are no losses in metabolizing the digestible fats and carbohydrates. These differences in digestibility between human food stuffs and cattle and rabbit feeding stuffs are presumably due to differences in the physical nature of the respective diets, while the fermentation processes in the digestive tract of ruminants are responsible for further depressions in the metabolizable energy (or physiological fuel value) in these species. The physiological fuel values (or metabolizability) of carbohydrates and proteins of cattle and rabbit feeding stuffs are perhaps more nearly 2.5 Calories per gram than 4 Calories; and of fat 5.7 to 6 Calories per gram than 9 Calories, the exact values depending on the physical nature (cellulose structure, etc.) of the feeding stuffs. It would perhaps be more con-



venient, and simpler, to compute rations for farm animals on the basis of the physiological fuel values than net energy values; for while, undoubtedly, there is much variability in physical structure, and therefore physiological fuel values, of the feeding stuffs, this is at least nearly constant for a given feeding stuff, while the specific dynamic action—and therefore the net energy—varies enormously with the plane of nutrition.

**2. Changes in Digestibility, Metabolizability, and Utilizability (net energy) with Increase in the Dietary Gross Energy.**—In Fig. 3 we have represented the *averages* of the digestibility, etc., of the rations fed to the steer and rabbit. In Fig. 4 we have plotted on arithlog paper the digestibilities etc., of each animal separately as functions of the respective gross energy and dry matter intakes. The curves are numbered separately in the upper and lower halves of the chart, and legends are given for each number.

The digestibilities of the fiber (curve 7 in the upper half of Fig. 4) on the several planes of nutrition show a more or less regular decline in the case of Mitchell's steer; but they do not show regularity of change in the case of Forbes' steers.

The digestibility of the ether extract (curve 6) tends to show a rise from  $\frac{1}{2}$  to 1 maintenance in the case of Forbes' steers, then it tends to decline more or less regularly. Mitchell's curve shows a continuous decline from the lowest to the highest plane of nutrition.

The digestibilities of organic matter, dry matter, and carbon are quite parallel on this arithlog paper; and following the maintenance level, decline more or less regularly. The steer curves are more regular than the rabbit curves.

The digestibility of the "N-free extract" declines in orderly fashion with the increase of the plane of nutrition.

Now, turning to the lower half of Fig. 4, it is seen that following the maintenance level, the digestible energy, digestible less methane energy, and metabolizable energy (Curves 1, 2, and 3) decline in orderly fashion; the decline in the digestible energy (Curve 1) is rather steeper than in the metabolizable energy. While the curves representing Forbes' data rise from  $\frac{1}{2}$  to 1 maintenance, the curves of Mitchell's data decline continuously from the lowest to the highest plane of nutrition. As before, the curves of Wiegner's data for the rabbit are relatively less regular than the steer curves.

The net energy curves (No. 4, lower half of the chart) are the steepest of all, thus emphasizing the influence of the S. D. A. factor on the relationship between the plane of nutrition and net energy.

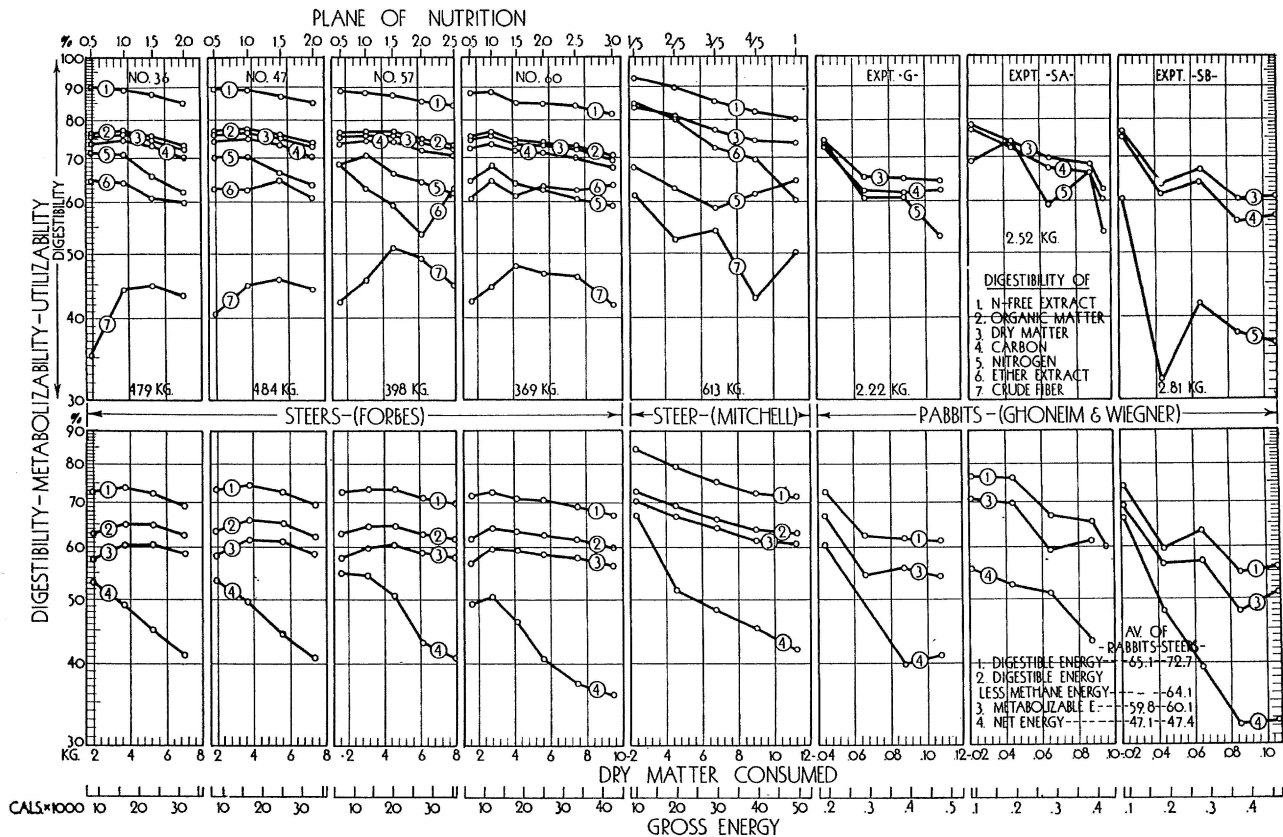


Fig. 4.—Coefficients of digestibility (upper half) and percentages of gross energy intake as digestible energy, digestible energy less methane energy, metabolizable energy, and net energy (lower half), plotted as functions of dietary gross energy and dry matter in steers and rabbits. See legends on charts, and text, for detailed explanations. The planes of nutrition (upper axis) are represented in the case of Forbes' steers, in terms of gross energy at maintenance; in the case of Mitchell's steer, they are represented in terms of gross energy at "full feed".

**3. Changes in the Several Losses With Increase in the Dietary Gross Energy.**—It appeared from Fig. 4 that the S. D. A. is probably the most important factor in decreasing the net energy value of a feeding stuff with the increase in the plane of nutrition. We have plotted on arithlog paper in Fig. 5 the percentage ratios (with respect to gross energy intake) of the energy losses in the form of S. D. A., urine, methane, and feces as functions of gross energy and dry matter intake. This is done in order to bring out the same ideas as in Fig. 4, but in a more direct fashion.

It is seen in Fig. 5 that the slopes (percentage changes) of the curves for urine, methane, and feces are slight in comparison to the slopes of the S. D. A. curves. The energy losses in the form of S. D. A. rise steeply from about 3% on the  $\frac{1}{2}$ -maintenance ration to about 20% on 3-maintenance ration, while for feces the range is only from about 26% to 32%. The range for methane and urine is still less. The absolute losses are greatest for feces (about 25% of the gross energy); followed by the S. D. A. losses (10-20% of the gross energy); followed by the methane loss (about 9% of the gross energy). The urinary loss is least (3 to 5% of the gross energy, depending presumably largely on the relative nitrogen intake).

It is difficult to explain the differences in shape of the several curves (feces, S. D. A. and urine) between Mitchell's and Forbes' steers, unless it be due to experimental errors. Forbes' curves appear to be very consistent indeed. Steers 36 and 47 are seen (in Fig. 5) to give almost identical results, as do also steers 57 and 60.

For purposes of comparison, the curves of digestible energy, metabolizable energy, and net energy, expressed as percentages of gross energy intake which are shown in the lower half of Fig. 4, are again repeated in the upper part of Fig. 5. The total heat production is also here given. It is interesting to note that at the (one) maintenance level the total heat production is only 60% of the gross energy intake; 40% of the dietary energy is thus clearly shown to be lost in the several ways indicated by the lower curves.

**4. The Partition of the Several Losses and Gains at Different Planes of Nutrition.**—The relations between energy losses and energy intake are perhaps more clearly indicated in Fig. 6. This also gives the partition of the several gains and losses at different planes of nutrition. In this figure, nutrients ingested are plotted against planes of nutrition in terms of gross energy at maintenance (Forbes' steers) or at "full feed" (Mitchell's steer). The ordinates between the net energy curve and the axis of abscissae represent the net energy; similarly the ordinates between metabolizable and net energy represent losses due to S. D. A.; between

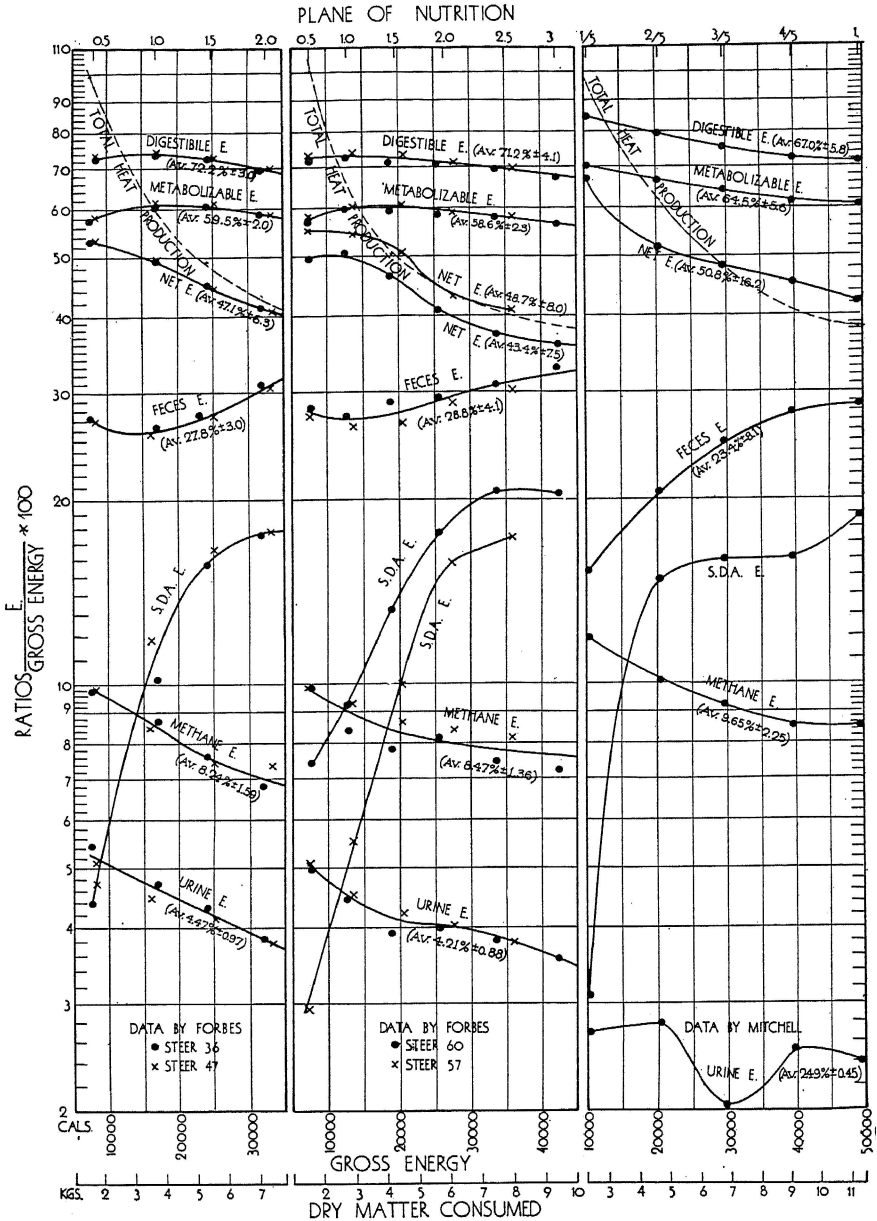


Fig. 5.—The several losses (urine, methane, S.D.A., and feces) expressed as percentages of gross energy intake; also the net, metabolizable, and digestible energies expressed in terms of percentages of gross energy intake; also, total heat production in terms of percentage of gross energy intake. The planes of nutrition (upper axis) are represented in the case of Forbes' steers in terms of gross energy at maintenance; in the case of Mitchell's steers they are expressed in terms of gross energy at "full feed".

digestible less methane and the metabolizable energy, they represent the energy of the urine. Between digestible, and digestible less methane energy they represent the methane energy; between gross and digestible energy they represent the energy of the feces.

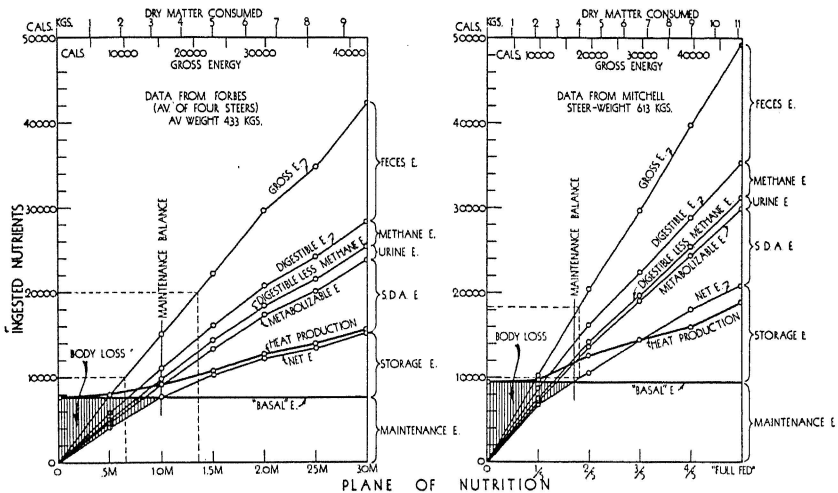


Fig. 6.—The relations between the plane of nutrition and the energy losses in the forms of feces, methane, urine, S.D.A.; also energy storage (fattening) following the maintenance level, and body losses preceding the maintenance level. Note that the gains or losses at any point of food ingestion are determined by the lengths of the ordinates at the given point between the indicated limits. Note that at the maintenance level the net-energy curve crosses the “basal” metabolism curve, and the metabolizable-energy curve crosses the total heat production (basal plus S.D.A. energy) curve. See Table II for the numerical values computed from these curves.

Thus, if it is desired to determine the numerical losses or gains respectively at the gross-energy intake level of 10,000 and 30,000 Calories, horizontal lines are drawn from the 10,000 and 30,000 levels indicated by the axis of ordinates until they meet the gross-energy line; the lines are then dropped vertically to the zero line, as shown in Fig. 6 by the fine broken lines. The lengths of the ordinates thus give directly the several losses or gains. In like manner, to determine the gross, digestible, etc., energies corresponding to a given value of net energy, a vertical line is drawn from the given point on the net-energy curve to the gross-energy curve, then horizontally to the axis of ordinates which gives the desired numerical value.

• Attention should be called perhaps, to the fact that at the point of energy equilibrium, in Fig. 6 and 7, the net energy curve crosses the “basal” metabolism curve, and the metabolizable-energy curve crosses the heat-production curve. These facts follow from the definitions of “basal” metabolism, net-energy, and metabolizable energy.

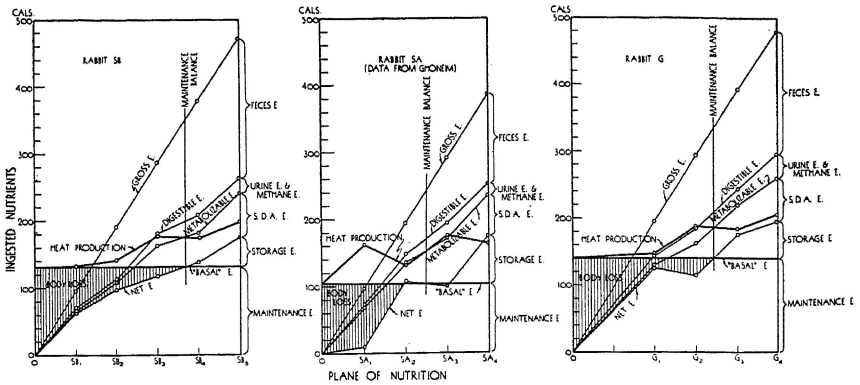


Fig. 7.—A continuation of Fig. 6, but as it relates to the rabbit.

5. **The Significance of the Plane of Nutrition.**—At the maintenance level of nutrition the animal is, of course, in energy equilibrium. According to the net-energy conception, the net-energy of the ration equals the *postabsorptive* heat production; that is, it equals to the heat produced by the animal less the heat of S. D. A.; or the *metabolizable* energy of the diet (physico-logical fuel values of Sherman) equals to the total heat production.

These ideas, as previously noted, are illustrated graphically in Figs. 6 and 7, by the fact that at the maintenance level the net-energy curve crosses the basal-metabolism curve; and the metabolizable-energy curve crosses the heat production curve. So much for the 1-maintenance level.

Now, what is meant by the 2-maintenance level? When Forbes fed his animals double the amount of *gross-energy* that he fed at 1-maintenance, then he called it 2-maintenance. This is one way of defining 2-maintenance. Perhaps a more rational definition of two-maintenance, according to the net-energy conception, is that the 2-maintenance plane of nutrition contains twice the amount of *net-energy* required at 1-maintenance; or that plane of nutrition which supplies net-energy double the “basal” metabolism (really double the post-absorptive heat production). Similarly at 3-maintenance the net-energy of the ration is equal to 3-times the “basal” metabolism. This appears to us to be a more consistent arrangement, and so in Figs. 11 and 12 the planes of nutrition are represented in terms 1 B (basal), 2 B, etc., where 1 B and 2 B are respectively the heat productions at “basal” metabolism and twice basal metabolism.

6. **The Relation Between the Heat Increment (S. D. A.) and Dietary Intake.**—In Fig. 8, we have plotted on the lower half of the chart

heat increments, or S. D. A., (that is, heat production above the "basal" level) as functions of gross energy (Curves A), digestible energy (Curves B), metabolizable energy (Curves C), nitrogen ingested (Curve D), and urinary nitrogen above the "basal" level (Curve E). As we pass from A to C, the curves become steeper, and more linear in shape.

Continuous curves A to C, which represent the averages of Forbes' four steers, do not indicate the presence of declines in the upper segments of the curves—declines which were strongly emphasized by Forbes in his discussion of the curves of the individual animals.

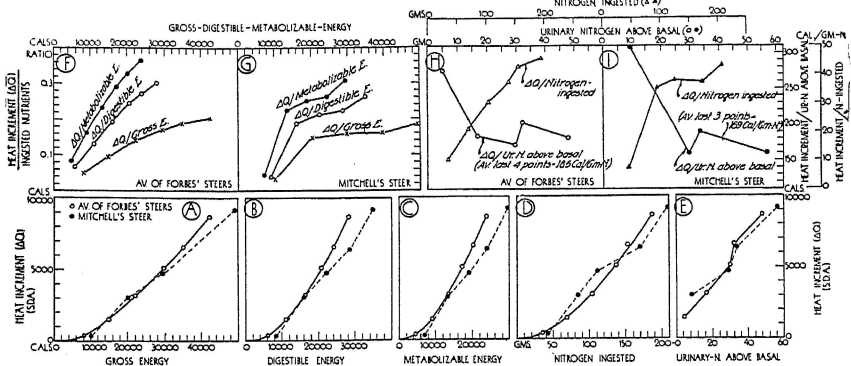


Fig. 8.—The lower half of the chart represents heat production above "basal" plotted against gross, digestible, metabolizable energy and nitrogen in the feeding stuffs; the upper half of the chart represents the ratios of heat production (ΔQ) above the "basal" level to the gross, digestible, metabolizable energy (E) and nitrogen in the feeding stuffs. The ratios of heat production above basal (ΔQ) to urinary nitrogen are also shown.

Broken curves A to C, representing Mitchell's steer, are less orderly as regards the distribution of the data points, but they certainly fail to show a decline in the upper regions. In other words, these curves fail to substantiate Forbes' contention that the heat production curve is S-like in form. On the contrary, it appears from Fig. 8, that the slope increases continuously. This is in agreement with what might be predicted from the theories of S. D. A.

The upper half of Fig. 8, represents the same data in the form of ratios of heat increment (above basal) to gross, digestible, and metabolizable energy intake (Curves F and G), and to nitrogen ingested and urinary nitrogen excreted (curves H and I). It is evident, as might be expected, that the curves of the ratios of heat increments to digestible energy are more linear than the gross-energy curves, and the curves for metabolizable energy are more linear than the digestible energy curves.

The ratios of heat increment to urinary nitrogen excretion are unusually high as compared to the heat increments for the dog represented in Fig. 1. It will be recalled that for the dog (Fig. 1), the ratio of

heat production above basal to urinary nitrogen above basal is of the order of 11 Calories per gram of nitrogen. In the case of steers, on the other hand, as shown in Fig. 8, this ratio is of the order of 180 Calories per gram of urinary nitrogen (not including the first high point). However, the heat production of the dog was measured under conditions of absolute rest, while the steers could stand or lie, or sway their bodies at will. The ratio of the high heat increment to urinary nitrogen excretion in the steers must therefore be attributed either to extreme relative restlessness of the animals after feeding as compared to the fasting state; or to a high S. D. A. of the non-protein feeding stuffs; or to expenditure of energy associated with the muscular work of mastication, peristaltic movements, etc., in these herbivorous animals handling bulky roughages. Benedict's acid-body theory of S. D. A. may ultimately be useful in the explanation of the differences in S. D. A. between the dog and steer.

**7. The Mathematical Function Relating the Net-Energy of a Feeding Stuff with the Level of Dietary Intake.**—As previously noted, Armsby and Kellner assumed that the net energy value of a ration may be defined by a constant; Mitchell concluded that the net value of a ration is not a constant but is defined by a linear equation relating it to the intake of dry matter; Forbes concludes that there is an "existence of a fundamentally different net-energy value of a feeding stuff at each point of observation, in relation to the plane of nutrition"; Wiegner and Ghoneim, on the basis of theoretic considerations, proposed an exponential equation relating net energy per unit area with the metabolizable energy per unit area. What might be the "true" functional relations between these variables?

We have plotted in Fig. 9 (A and B) net energy as functions of metabolizable, digestible, and gross energy. It is there seen that the curve relating net to gross energy has the most curvature, while the curve relating net to metabolizable energy has the least curvature. This applies to Mitchell's as well as to Forbes' data. In our opinion none of the curves are linear, that is, all of them have distinct downward curvatures. This opinion, which is based on the shape of the curves, is in agreement with the general theory of S. D. A. We therefore differ from Mitchell in that while Mitchell believes this relation to be linear, we believe it to be non-linear.

We believe that Wiegner was theoretically and practically in the right in proposing an exponential relation between net energy and metabolizable energy; but we believe that Wiegner's proposal may be bettered by applying the exponential equation for relating net with gross (rather than with metabolizable) energy, and for the following reason: By relating net with metabolizable energy as was done by Wiegner, it is tacitly assumed that the *only* cause of the decline in the net energy with



the increase of the plane of nutrition is due to increased S. D. A.; as a matter of fact the decline is due not only to increased S. D. A. (as would be predicted from the theories of S. D. A.) but also to decreased digestibility, and to a less extent to decreased metabolizability of the digested food, as may be seen from *a* and *b* in Fig. 9. It therefore seems to us to be most logical to relate by an exponential equation the net energy with the gross (not metabolizable) energy; and this we now propose to do.

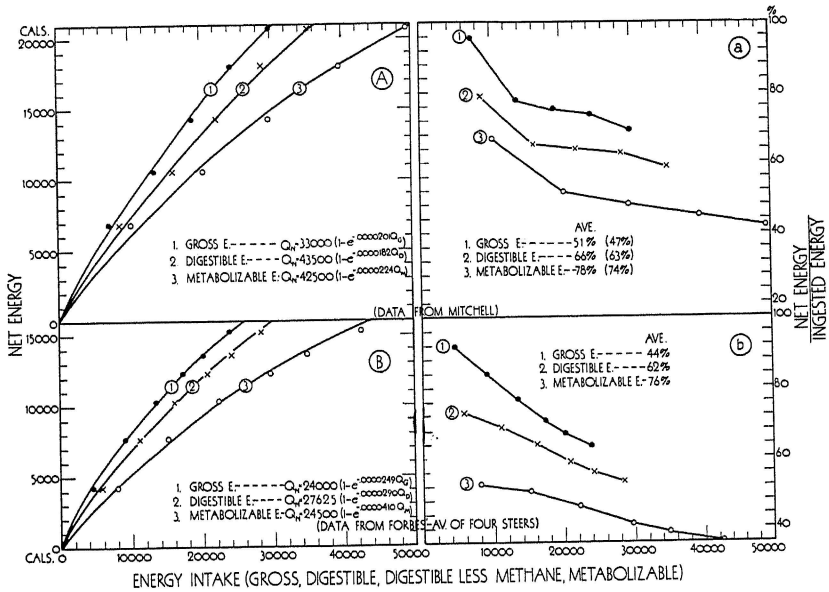


Fig. 9.—Net energy as function of gross, digestible, digestible less methane, and metabolizable energy. Curves A and B represent respectively Mitchell's and Forbes' (average) steer data; Curves *a* and *b* represent the percentage ratios of net energy to gross, digestible, digestible less methane, and metabolizable energy for Mitchell's and Forbes' steers. In Curves *a*, the values in parentheses represent the ratios with the  $\frac{1}{2}$ -plane omitted. Note the break in Mitchell's datum is too high on account of an experimental error (see text for the theoretical significance of such an error if present, in deciding the proper junctional relation between net and gross energy).

We prefer to use the same *form* of this exponential equation as we have used before to represent growth and metabolism, thus

$$Q_n = A(1 - e^{-kQ_g}) \tag{3}$$

in which  $Q_n$  is the net energy;  $Q_g$  is the gross energy;  $A$  is the maximum value of  $Q_n$  for the given animal and ration;  $k$  is the relative (or when multiplied by 100 the percentage) decline of  $Q_n$  with increasing values of  $Q_g$ ;  $e$  is the base of natural logarithms.

We have fitted this equation to Forbes' and Mitchell's steers with the results shown in Fig. 10 (and, also, in Fig. 9). The agreement between observed and computed values is very satisfactory as far as it relates to Forbes' steers. As far as the data for Mitchell's steer are concerned, the datum for the  $\frac{1}{2}$  plane appears to be too high; therefore, two

equations were fitted to these data one including (Curve A) and the other omitting (Curve B) the 1/5-plane datum.

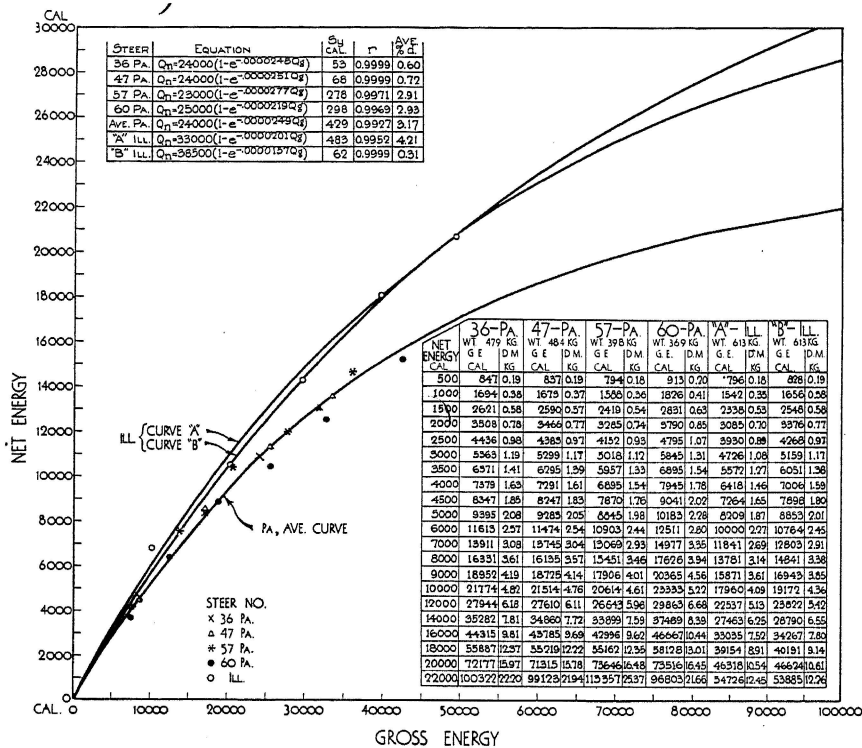


Fig. 10.—Net energy as function of gross energy intake. The data points represent the observed values; the smooth curves represent the equations given in the upper-left table. In the equations, Q<sub>n</sub> represents the net energy, Q<sub>g</sub> the gross energy, and e the base of natural logarithms. Curve "A" includes all of Mitchell's data, curve "B" omits the first (1/5-plane) datum. S<sub>y</sub> includes 68% of the observed data; r represents the correlation coefficients for the several curves. See text for full discussion. The lower-right table gives computed values for gross energy and dry matter corresponding to different values of net-energy. The values were computed from the given equations on the upper-left table.

The equations, with their statistical constants, are given on the chart (Fig. 10). The significance of the coefficients of correlation, r, is doubtful in view of the small number of data points and the non-linear nature of the equation. The magnitudes of the percentages of deviation, d, are satisfactory, as are, also, the magnitudes of the standard error, S<sub>y</sub> (68% of the data fall within ±S<sub>y</sub>). The large table in Fig. 10, gives computed values of gross energy and dry matter for each of the animals corresponding to given values of net energy.

In order to demonstrate concretely that the simple exponential equation represents the data better than linear or simple parabolic equations, we have fitted these three equations to Forbes' and Mitchell's data, and then computed the deviations. The results are shown in Table 3. Table 3 shows the unquestionable superiority of the exponential

TABLE 3

Net Energy vs.	Type of Equation	STEER 36-PA.		STEER 47-PA.	
		Equation	Deviation Av. %	Equation	Deviation Av. %
Gross Energy Digestible Energy	Exponential	$Q_n = 24000(1 - e^{-0.000245Q_n})$	0.60	$Q_n = 24000(1 - e^{-0.000251Q_n})$	0.72
	Parabolic	$Q_n = 2.962Q_n^{.812}$	2.19	$Q_n = 3.416Q_n^{.738}$	2.56
	Linear	$Q_n = 1738 + .366Q_n$	4.18	$Q_n = 1825 + .363Q_n$	4.66
	Exponential	$Q_n = 29500(1 - e^{-0.000285Q_n})$	0.65	$Q_n = 28500(1 - e^{-0.000278Q_n})$	0.47
	Parabolic	$Q_n = 2.80Q_n^{.846}$	1.03	$Q_n = 3.14Q_n^{.834}$	1.11
Metabolizable Energy	Linear	$Q_n = 1346 + .539Q_n$	2.02	$Q_n = 1437 + .531Q_n$	2.51
	Exponential	$Q_n = 24000(1 - e^{-0.000419Q_n})$	0.99	$Q_n = 25000(1 - e^{-0.000395Q_n})$	1.19
Energy	Parabolic	$Q_n = 5.31Q_n^{.795}$	0.91	$Q_n = 5.15Q_n^{.798}$	0.95
	Linear	$Q_n = 1693 + .620Q_n$	2.55	$Q_n = 1681 + .618Q_n$	2.44
Net Energy vs.	Type of Equation	STEER 57-PA		STEER 60-PA	
		Equation	Deviation Av. %	Equation	Deviation Av. %
Gross Energy Digestible Energy	Exponential	$Q_n = 23000(1 - e^{-0.000277Q_n})$	2.91	$Q_n = 25000(1 - e^{-0.000219Q_n})$	2.93
	Parabolic	$Q_n = 3.517Q_n^{.798}$	4.93	$Q_n = 3.692Q_n^{.783}$	6.74
	Linear	$Q_n = 2183 + .357Q_n$	6.96	$Q_n = 2125 + .315Q_n$	6.45
	Exponential	$Q_n = 26000(1 - e^{-0.000326Q_n})$	2.33	$Q_n = 26500(1 - e^{-0.000359Q_n})$	3.06
	Parabolic	$Q_n = 3.70Q_n^{.820}$	3.85	$Q_n = 3.41Q_n^{.820}$	3.58
Metabolizable Energy	Linear	$Q_n = 1864 + .520Q_n$	5.67	$Q_n = 1751 + .476Q_n$	5.16
	Exponential	$Q_n = 23500(1 - e^{-0.000456Q_n})$	2.11	$Q_n = 25500(1 - e^{-0.000388Q_n})$	2.38
Energy	Parabolic	$Q_n = 5.36Q_n^{.798}$	3.63	$Q_n = 4.86Q_n^{.799}$	3.06
	Linear	$Q_n = 2014 + .620Q_n$	5.66	$Q_n = 1889 + .562Q_n$	5.05
Net Energy vs.	Type of Equation	ILL-STEER "A"		ILL-STEER "B"	
		Equation (1st datum included)	Deviation Av. %	Equation (1st datum omitted)	Deviation Av. %
Gross Energy Digestible Energy	Exponential	$Q_n = 33000(1 - e^{-0.000201Q_n})$	4.21	$Q_n = 38500(1 - e^{-0.000157Q_n})$	0.31
	Parabolic	$Q_n = 7.20Q_n^{.738}$	2.10	$Q_n = 1.69Q_n^{.876}$	3.12
	Linear	$Q_n = 3314 + .360Q_n$	1.76	$Q_n = 3590 + .353Q_n$	1.83
	Exponential	$Q_n = 43500(1 - e^{-0.000182Q_n})$	3.28	$Q_n = 58500(1 - e^{-0.000125Q_n})$	1.08
	Parabolic	$Q_n = 4.61Q_n^{.803}$	2.03	$Q_n = 2.19Q_n^{.876}$	1.54
Metabolizable Energy	Linear	$Q_n = 2194 + .534Q_n$	1.73	$Q_n = 2134 + .536Q_n$	2.00
	Exponential	$Q_n = 42500(1 - e^{-0.000224Q_n})$	3.50	$Q_n = 54500(1 - e^{-0.000161Q_n})$	1.02
Energy	Parabolic	$Q_n = 6.12Q_n^{.788}$	2.24	$Q_n = 2.83Q_n^{.865}$	1.23
	Linear	$Q_n = 2343 + .624Q_n$	1.52	$Q_n = 2246 + .628Q_n$	1.72
Net Energy vs.	Type of Equation	RABBIT-SB		RABBIT-SA	
		Equation	Deviation Av. %	Equation	Deviation Av. %
Gross Energy Digestible Energy	Exponential	$Q_n = 130(1 - e^{-0.0065Q_n})$	1.57	$Q_n = 275(1 - e^{-0.00243Q_n})$	3.97
	Parabolic	$Q_n = 7.015Q_n^{.456}$	1.76	$Q_n = 1.102Q_n^{.854}$	3.19
	Linear	$Q_n = 47.7 + .209Q_n$	5.05	$Q_n = 20.6 + .402Q_n$	7.06
	Exponential	$Q_n = 150(1 - e^{-0.00795Q_n})$	1.69	$Q_n = 410(1 - e^{-0.00265Q_n})$	5.92
	Parabolic	$Q_n = 5.199Q_n^{.594}$	2.88	$Q_n = 0.815Q_n^{.972}$	4.33
Metabolizable Energy	Linear	$Q_n = 38.6 + .410Q_n$	3.90	$Q_n = 6.87 + .663Q_n$	5.36
	Exponential	$Q_n = 165(1 - e^{-0.00733Q_n})$	1.01	$Q_n = 415(1 - e^{-0.00221Q_n})$	6.85
Energy	Parabolic	$Q_n = 4.488Q_n^{.635}$	1.87	$Q_n = 0.883Q_n^{.973}$	5.77
	Linear	$Q_n = 33.7 + .492Q_n$	2.86	$Q_n = 9.81 + .705Q_n$	7.49

equation as far as Forbes' data are concerned; and, also, for Mitchell's data if the first ( $\frac{1}{5}$ -plane) datum is omitted. As previously noted, Mitchell's  $\frac{1}{5}$ -plane datum appears rather too high (see e. g., curves G in Fig. 8, or curves *a* in Fig. 9). It is, of course, possible, and it seems probable, from the break in Mitchell's curves between  $\frac{1}{5}$  and  $\frac{2}{5}$ -planes in the aforecited examples, that the  $\frac{1}{5}$ -plane datum is too high on account of an experimental error. It is for this reason that we thought it necessary to fit two curves to Mitchell's data, one including (Curve A) and one omitting (Curve B) the first datum. As previously noted, Wiegner's data are less orderly in their distribution (See Fig. 9) than either Forbes' or Mitchell's data, and so we have not fitted equation (3) to the rabbit data.

**8. The Influence of Body Weight on the Relation Between Net and Gross Energy.**—Increasing food intake tends to decrease digestibility, metabolizability, and utilizability (net energy) of the feeding stuff. The foregoing analyses made this quite certain and obvious. If the exponential equation represents the functional relation between net and gross energy, then the ratio of net to gross energy varies directly with the distance from the given level of net-energy intake to the maximum net-energy intake capacity of the animal. Now it is obvious that the maximum intake capacity of an animal varies with its size; therefore, the size of the animal must be an important factor influencing the net-energy value of a given *amount* of intake of feeding stuff. The ingestion of 0.2 kilos of dry matter, for example, is a large amount for a rabbit, while the ingestion of even 2 kilos is an insignificant amount for a large steer.

The above ideas are illustrated in Fig. 11. On the left side the net-energy intakes, in terms of percentage of the maximum net-energy capacity (A in our exponential equation (3)), are plotted against gross energy intakes. The curve for the rabbit is seen to be exceedingly steep, the curve for Mitchell's large steer is quite flat, while the curve of Forbes' medium-sized steer is intermediate. On the right side, given net-energies, in terms of percentages of the net energies at 1-maintenance, are plotted against planes of nutrition in terms of 1, 2, etc., "basal" (B) metabolism. In this case, the data for the rabbits and all steers coincide.

A way might be found for including into equation (3), the body size factor. If the ratio of the maximum net-energy intake to body weight were constant, then, of course, equation (3) could be written in the form

$$Q_n = \frac{A}{m}(1 - e^{-kQ_g})$$

in which *m* is body weight.

It is not now possible to say whether or not this ratio, or some other ratio, such as, for example,  $A/S$  where *S* is surface area, is constant

because the range in body weights of the animals is not wide enough. It is certain, however, that body size is an important element in the evaluation of the relation between net and gross-energy for given absolute amounts of food intake. But, if the data are plotted as on the right side of Fig. 11 (ratio of net-energy to maintenance net-energy plotted

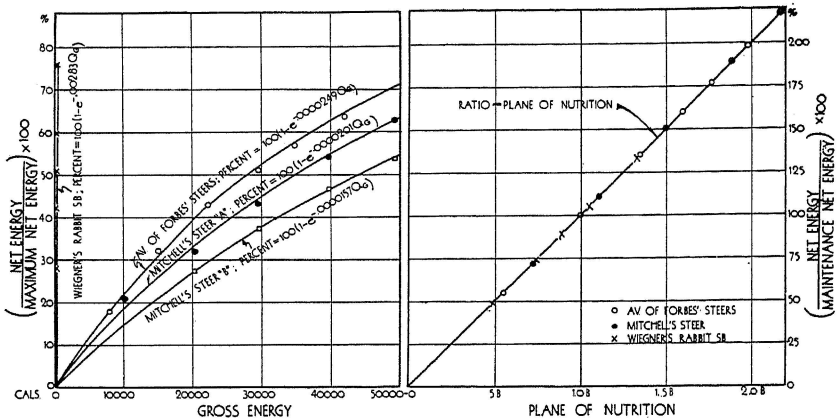


Fig. 11.—On the left side the ratios of net-energy to the maximum net-energy intake (A in equation (3)) are plotted against gross-energy intake; here the rabbit curve is very steep in comparison to the steer curve, indicating in graphic manner that the size of the animal is a decisive factor in the problem of evaluation of the net energy of a given amount of feed. But if the net energy/maintenance net-energy ratios are plotted against 1B, 2B, etc., in which 1B is "basal" heat production, 2B is twice basal heat production, etc., then all data coincide.

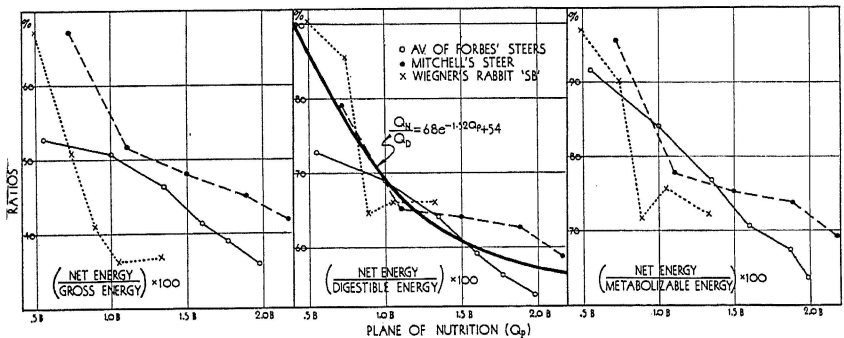


Fig. 12.—The energy ratios of net to gross, net to digestible, net to metabolizable, are here plotted against 1B, 2B, etc., (where B stands for the basal heat production, twice basal, etc.) metabolism. Note that the curves in the middle chart (net to digestible) are quite close together.

against 1, 2, etc., times the basal heat production), then the rabbit and steer data coincide (ratio of net energy to maintenance net energy equals to the plane of nutrition). Approximate correspondence may also be ob-

tained by plotting the ratio of net energy,  $Q_n$ , to digestible energy,  $Q_d$ , against the plane of nutrition,  $Q_p$ , as shown in Figs. 12 and 13. The equation for this relation is

$$Q_n/Q_d = 43e^{-Q_p} + 54$$

indicating that this ratio approaches 54% as limit; that is, the net energy never falls below about 54% of the digestible energy.

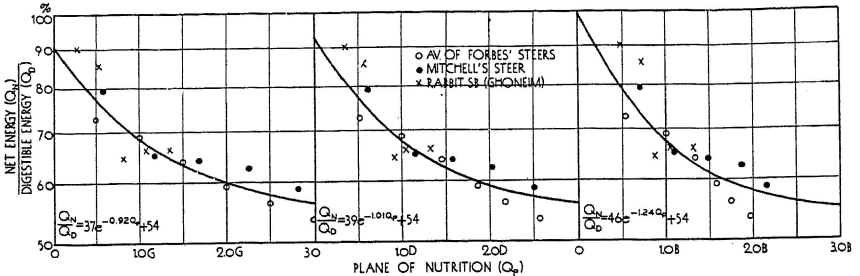


Fig. 13.—Ratios of net energy to digestible energy of the steer and rabbit data plotted against planes of net nutrition expressed in terms of 1, 2, etc., times gross energy intake (1G, 2G, etc.); digestible energy (1D, 2D, etc.), and “basal” energy (1B, 2B, etc.) intake with the corresponding equations. The data are plotted on arithlog paper. Note that the rabbit and steer data nearly coincide.

### SUMMARY AND CONCLUSIONS

This bulletin is concerned chiefly with a critical discussion of the variations of net energy of feeding stuffs with increases in the plane of nutrition. Since such variations in net energy depend largely on variations in the heat of specific dynamic action (S. D. A.), therefore a very substantial part of this paper is given to a discussion of the theories and facts of the phenomenon of specific dynamic action.

The analysis of the specific dynamic action problem leads to the following conclusions:

1. Zuntz' theory of “intestinal work” when taken in a broad sense, as Zuntz meant it to be taken to include the energy expense of secretion and excretion, appears to account for a large part, but not all, of the energy of specific dynamic action.

2. It appears from the results of Grafe, Lundsgaard, Krebs, and Borsook that the formation of urea from its precursors is associated with a considerable oxygen consumption. These oxidations, appear from the work of Krebs and Borsook, to be the result not of “the energy necessary, but the stoichiometrical relationship” (Borsook) involved. In other words, ureagenesis appears to be an important contributing factor to the phenomenon of specific dynamic action of proteins, or even of inorganic salts which are excreted in the form of urea. The con-

tribution of ureagenesis to S. D. A., must be classed under Rubner's general theory. Little of a very definite nature can be said at this time concerning the contributions to S. D. A. of the energy of deamination and of glucose formation from amino acids, even though the current investigations in this field by a group of very brilliant bio-physical chemists are exceedingly suggestive and interesting.

3. It appears that the S. D. A. of fats and carbohydrates is due in part to "intestinal work" in the broad Zuntz' sense, and in part to the chemical law of mass action which accelerates the oxidation of these substances with their increase in concentration. The energy losses associated with fermentation of carbohydrates appears to be an important contributing factor, at any rate, in ruminants. There may be an energy expense associated with the conversion of carbohydrates to fats, but little is known about this; there may also be an energy loss associated with the formation of glycogen from glucose, or glucose from glycogen.

5. Cattle or other farm animals which can not be trained to be absolutely quiet, may give apparently unusually high values for S. D. A. on account of the fact that these animals tend to be more lively, more restless, after feeding than during the post-absorptive condition. In case of ruminants, the physical work of mastication, peristalsis, etc., is probably also a very substantial contributing factor to the S. D. A. in these animals.

6. The question as to whether or not Voit's (and also Benedict's and Grafe's) "stimulating" theory can account in part for the phenomenon of S. D. A. can not at present be answered; and so this must await further accumulation of data in this field.

The analysis of the net-energy problem in cattle and rabbits leads to the following conclusions:

1. The digestibility of typical rations in these animals is very low compared to digestibilities of diets in humans (as quoted by Sherman). About 28 per cent of the gross ingested energy in these animals is lost in the form of feces. These losses increase more or less (depending on the nature of the ration) with the increase in the plane of nutrition. The range of increases in the losses with the increase in the plane of nutrition is not, however, very great (range 5 to 10%).

2. The methane losses in ruminants are quite considerable (about 9% of the gross energy); but the range in losses from the lowest to the highest plane is not very great (range about 3%).

3. The energy loss in urine is rather small (about 5% of the gross energy) and the range in losses from the lowest to the highest plane is quite small (about 1.5%).

4. The range in energy losses due to specific dynamic action vary enormously with the plane of nutrition (ranging from about 3% of the

gross-energy at about  $\frac{1}{2}$  maintenance to about 20% of the gross energy at maximum feed intake).

5. The net-energy per unit ration intake thus declines with increasing plane of nutrition largely on account of the increase in specific dynamic action.

6. It is shown that the net energy,  $Q_n$ , changes with the intake of gross energy,  $Q_g$ , in a given animal according to the equation

$$Q_n = A(1 - e^{-kQ_g})$$

in which  $A$  is the maximum net-energy intake capacity,  $k$  is the relative (or when multiplied by 100, percentage) change of  $Q_n$  with changing intake of  $Q_g$ ,  $e$  is the base of the natural system of logarithms.

7. In the above equation, the numerical constants vary with the size of the animal. In order to eliminate the size factor it is necessary, first, to divide  $A$  in the above equation by weight, area, or some other equalizing size factor (nature of this factor has not yet been determined on account of paucity of data); second, plotting  $Q_n$  not against the *amounts* of feed consumed, but against the plane of nutrition (1-maintenance, 2-maintenance, etc.).

8. Since the problem in 7 above has not yet been solved, we have plotted the ratio of net to digestible energy ( $Q_n/Q_d$ ) against the plane of nutrition ( $Q_p$ ). The steer and rabbit data in this case nearly coincided and the equation for the curve was found to be

$$Q_n/Q_d = Ae^{-kQ_p} + 54$$

indicating that the net energy can never fall below (with these types of rations and animals) 54% of the digestible energy.

Or, the ratio of net energy to net energy at maintenance may be plotted against the plane of nutrition (in terms of 1, 2, etc., of the basal metabolism) as shown in Fig. 11 in the text, when the ratio equals to the plane of nutrition. In this case the rabbit and steer data coincide absolutely.



## BIBLIOGRAPHY

- Adams. *Specific dynamic action from the standpoint of the second and third laws of thermodynamics.* J. Biol. Chem., 1926, 67, p. XXI.
- Anderson and Lusk. *The interrelation between diet and body condition and the energy production during mechanical work.* J. Biol. Chem., 1917, 32, 421.
- Armsby. *The nutrition of farm animals.* New York, 1917.
- Artundo. *Specific dynamic action in hypophysectomized dogs.* C. R. Soc. Biol. 1931, 106, 139.
- Atkinson and Lusk. *Further experiments relative to the cause of the specific dynamic action of protein.* J. Biol. Chem., 1918, 36, 415; *The influence of lactic acid upon metabolism.* Id., 1919, 40, 79.
- Aub, Everett and Fine. *The intravenous administration of amino acids to decerebrate and urethanized cats.* Amer. J. Physiol., 1927, 79, 559.
- Aubel. *Sur l'énergetique du métabolisme intermédiaire.* Bull. Soc. Sc. Hygiène Alimentaire, 1924, xii, 257-273; 416-422.
- . *Sur l'action dynamique spécifique.* Ann. de Physiol. et Physicochim. biol., 1924, I, 31.
- . *Sur l'action dynamique spécifique.* Id., 1927, iii, 121.
- . *Sur l'action dynamique spécifique de l'alanine.* C. R. Assoc. des Physiol. Ann. de Physiol. et Physicochim. biol., 1928, iv, n° 4.
- . *Über die spezifisch dynamische Wirkung des Alanins.* Biochem. Z., 1930, ccxxv, 81.
- et Schaeffer. *L'Action dynamique spécifique des protides.* Ann. de Physiol. et de physicochimie Biologique, 1932, 8, 262.
- Aubel et Wurmser. *Sur l'utilisation de l'énergie libérée par les oxydations.* C. R. Acad. Sc., 1924, 179, 848.
- Bacq. *Variations du métabolisme après injection intrapéritoneale.* Ann. Physiol. et Physicochimie biol., 1929, 5, 349.
- Barcroft and Brodie. *Gaseous metabolism of kidney.* J. Phys., 1905, 32, 18; *Gas metabolism of kidney,* Id., 1905-06, 33, 52.
- Barcroft and Straub. *Gas metabolism of the kidney,* Id., 1910, 41, 145.
- Benedict and Emmes. *The influence upon metabolism of non-oxidizable material in the intestinal tract.* Am. J. Physiol., 1912, 30, 197.
- Benedict and Pratt. *The metabolism after meat feeding of dogs in which pancreatic external secretion was absent.* J. Biol. Chem., 1913, 15, 1.
- Benedict and Ritzman. *The metabolism of the fasting steer,* Carnegie Institution of Washington, Publ. 377, 1927. See also Benedict, Trans. 15th Intern. Congress on Hyg. and Demography, Washington, D. C., 1912, 2, 394.
- Benedict. *Factors affecting basal metabolism.* J. Biol. Chem., 1915, 20, 253.
- and Carpentier. *Food ingestion and energy transformations, with special reference to the stimulating effects of nutrients.* Carnegie Institut. Publ., 1918, 261.
- Benedict and Benedict. *A permissible breakfast prior to basal metabolism measurements.* Boston Med. and Surg. J., 1923, 188, 849.
- Bonnet. *Grandeur de l'action dynamique spécifique en fonction de la température extérieure chez les Poikilothermes.* Ann. de Physiol. et Physicochimie biol., 1926, ii, 192; *Métabolisme énergétique et alimentation. Consommation de lux et Action dynamique spécifique.* Gap (France), 1929.
- Boothby and Sandiford. *The calorogenic action of adrenalin chloride.* Am. J. Physiol., 1923, 66, 93.
- Bornstein and Roese. *Über die Beeinflussung des Sauerstoffverbrauches überlebender Organe durch Glykokoll.* Untersuchungen zur Frage des Spez. dynam. Wirkung des Glykokolls. Pflüger's Archiv., 1929, 223, 498.
- Borsook and Winegarden. *On the free energy of glucose and of tripalmitin.* Proc. Nat. Acad. Sc., 1930, xvi, 559; *The work of the kidney in the production of urine.* Id., 1931, 17, 3; *The energy cost of the excretion of urine.* Id., 1931, 17, 13; *On the specific dynamic action of protein.* Id., 1931, 17, 75.
- Borsook and Keighly. *Energy of urea synthesis.* Science, 1933, 77, 114.
- Borsook and Schott. *The free energy, heat and entropy of formation of l-malic acid.* J. Biol. Chem., 1931, xcii, 559.
- Borsook and Huffman. *The free energies of formation of aqueous d-alanine, l-aspartic acid, and d-glutamic acid,* 1933, xcix, 663; see also J. Am. Chem. Soc. 1932, 54, 4297.

- Boyd, Hines and Leese. *Study of response to continuous intravenous injection of large amounts of glucose.* Am. J. Physiol., 1926, 74, 656.
- Carpenter and Fox. *The gaseous exchange of the human subject. I. As affected by the ingestion of water at 37°C. J. Nutrition, 1929-30, 2, 359; II. As affected by small quantities of dextrose.* Id., p. 375; *III. As affected by small quantities of Glucose.* Id., p. 389; *The influence of muscular work on the S. D. A. of glucose and fructose,* Arbeits physiologie, 1931, 7, 570.
- Cserna and Kelemen. *Beitrag zur Kenntnis der Spezifisch-dynamischen Wirkung der Nahrstoffe.* Bioc. Z., 1914, 66, 63.
- Csonka. *The rate at which ingested glycocoll and alanine are metabolized* J Biol. Chem., 1915, 20, 539; *On the administration of various proteins with benzoic acid to a pig.* Id., 1924, 60, 545.
- Cushny. *The secretion of urine.* London, 1926.
- Dann and Chambers. *The metabolism of glucose administered to the fasting dog.* J. Biol. Chem., 1930, 89, 675.
- Deuel. *The respiratory metabolism following the administration of various carbohydrates.* Id., 1927, 75, 367.
- Dock. *The relative increase in metabolism of the liver and other tissues during protein metabolism in the rat.* Amer. J. Physiol., 1931, 97, 117.
- Du Bois. *Basal Metabolism in health and disease.* Second edition, Philadelphia, 1927.
- Feder. *Der Zeitliche Ablauf der Zersetzung im Thierkorper.* Z. Biol., 1881, 17, 531.
- Fee and Hemingway. *The oxygen usage of the kidney.* J. Phys., 1928, 65, 100.
- Fingering. *Die Ernährung der landwirtschaftlichen Haustiere,* Handbuch der Landwirtschaft, Bd. IV, Lief. 10, Berlin, 1928.
- Firgau, Hartmann and Voit. *Ueber den Zeitlichen Ablauf der Stickstoffausscheidung bei Beifutterung von Kohlenhydraten zu Eiweiss.* Z. Biol., 1927, 85, 557.
- Forbes, Braman and Kriss, et al. *The energy metabolism of cattle in relation to the plane of nutrition.* J. Agr. Research, 1928, 37, 253; *Further studies of the energy metabolism of cattle in relation to the plane of nutrition.* Id., 1930, 40, 37.
- Forbes and Kriss. *The analysis of the curve of heat production in relation to the plane of nutrition.* J. Nutrition, 1932, 5, 183.
- Geelmuyden. *Ueber die spezifisch-dynamische Wirkung der Nahrungstoffe und ihre Beziehungen zum Grundumsatz beim Diabetes mellitus.* Ergebn. d. Physiol., 1925, 24, 1.
- Gephart and Du Bois. *The determination of the basal metabolism of normal men and the effect of food.* Arch. Int. Med., 1915, 15, 835.
- Ghonheim. *Ueber den Gesamtstoffwechsel bei Unternehmung und Produktionsfutter. Ein Beitrag zur Theorie der Futterwirkung bei Lebenderhaltung und Produktion und zur Methodik der Respirationsversuche.* Mitteilung aus dem Institut für Haustierernahrung an der Eidgenössischen Technischen Hochschule Zurich, 1930 (Vorstand Prof. Dr. G. Wiegner).
- Gibbons. *On the specific dynamic action of proteins in thin and fat individuals (dogs).* Amer. J. Physiol., 1924, 70, 26.
- Gigon. *Über den Einfluss von Eiweis und Kohlenhydratzufuhr auf den Stoffwechsel.* Skandin. Archiv. Physiol., 1908-09, 21, 351; *Über den Einfluss von Eiweis und Kohlenhydratzufuhr auf den Gaswechsel und Energieumsatz.* Pfluger's Archiv., 1909, 140, 509.
- Glaser, Laszlo, and Schürmeyer. *Blood flow and energy consumption of the kidney.* Klin. Wochschr. 1933, 12, 138.
- Grafe. *Beitrag zur Kenntnis der Ursachen der spezifisch dynamischen Wirkung der Eiweiskörper.* Deut. Archiv. Klin. Med., 1916, 118, 1; *Die spezifisch-dynamische Wirkung des Nahrungszufuhr.* Oppenheimers Handb. d. Biochem., 1926, 2nd edit., VI, 609.
- Hendricks. *Fitting the curve of the diminishing increment to the feed consumption-live weight growth curves.* Science, 1931, 74, 290.
- , Jull, and Titus. *A possible physiological interpretation of the law of the diminishing increment.* Id., 1931, 73, 427; *The utilization of feed by chickens,* Poultry Science, 1932, 11, 74.
- Honda. *Die Wirkung von Fleisch auf den respiratorischen Umsatz der mit Fett gefütterten Ratten, etc.* Bioc. Z. 1927, 185, 173; 191, 13-33 et 34-60.
- Hoobler. Am. J. Dis. Child., 1915, 10, 153.
- Janney. *The metabolic relationship of the proteins to glucose.* J. Biol. Chem., 1915, 20, 321.
- Jacquet. *Der respiratorische Gaswechsel.* Ergeb. d. Physiol., 1903, I, Abt. p. 457.

- Johansson, Billstrom und Heijl. *Kohlensaureabgabe bei Zufuhr verschiedener Zuckerarten*. Skand. Arch. Physiol., 1904, 16, 263.
- Johansson. *Untersuchungen über den Kohlehydratstoffwechsel*. Skand. Arch. Physiol., 1908-09, 21, 1.
- Johnston and Lewis. *Comparative Studies on the metabolism of aminoacids: I. Changes in the non-protein nitrogenous constituents of the blood following administration of aminoacids*. J. Biol. Chem., 1928, 78, 67.
- Johnston. *The specific dynamic response to protein of individuals suffering from disease of the hypophysis*. J. Clin. Invest., 1932, 11, 437.
- Jull and Titus. *Growth of chickens in relation to feed consumption*. J. Agric. Res., 1928, 36, 541. (See also Hendricks; Titus.)
- Kellner. *Die Ernährung der landw. Nutztiere*. Berlin, 1924.
- Khouvine, Aubel et Chevillard. *Sur la transformation de l'acide pyruvique en acide lactique dans le foie*. C. Rend. Acad. Sc., 1928, 189, 1102.
- Koraen. *Über den Einfluss der Nahrungsaufnahme auf den Stoffwechsel*. Skandin. Arch., 1901, 11, 176.
- Krauss und Rettig. *Studien zur spezifisch-dynamischen Nahrungswirkung. I. Die spezifisch-dynamische Eiweisswirkung des normalen erwachsenen Menschen*. Dtsch. Arch. Klin. Med., 1929, 163, 337.
- Krause und Kuppers. *Der Einfluss der Ernährungslage auf die Grösse des Grundumsatzes und der spezifisch dynamischen Nahrungswirkung*. Z. Klin. Med., 1931, 118, 64.
- Krebs. *The metabolism of amino acids in the animal body*. Klin. Wochschr., 1932, 11, 1744.
- Krummacher. *Das Gesetz der Isodynamen Vertretung und die spezifischdynamische Wirkung. Eine geschichtlich-kritische Untersuchung*. Ergeb. d. Physiol., 1928, 27, 188.
- Krzywanek. *Über den Einfluss der parenteralen Zufuhr einiger Aminosäuren auf den respiratorischen Gaswechsel des Hundes*. Bioc. Z., 1933, 134, 500
- Lefevre *Chaleur animale et bioenergetique* Paris, 1911.
- Liebeschütz-Plaut und Schadow. *Zur Ursache der spezifisch dynamischen Wirkung des Eiweiss*. Pflügers Archiv., 1926, 214, 537; *Zur Ursache der spezifisch-dynamischen Wirkung des Eiweisses. II. Die Zeitliche Beziehung zwischen spezifisch-dynamischer Wirkung und Eiweissstoffwechsel*. Id., 1927, 217, 717; *III. Die spezifisch-dynamische Eiweisswirkung bei aufgehobener Darminnervation*. Id., p. 733.
- Lublin. *Über den Einfluss der Nierenarbeit auf den Gaswechsel den Menschen*. Z. klin. Med., 1928-29, 109, 371.
- Lundsgaard. *Über die Ursachen der spezifischen dynamischen Wirkung der Nahrung*. I. Skand. Arch. Physiol., 1931, 62, 223; II. id., p. 243.
- Lusk. *The influence of the ingestion of aminoacids upon metabolism*. J. Biol. Chem., 1912, xiii, 155; *Metabolism after the ingestion of dextrose and fat, including the behavior of water, urea, and sodium chloride solution*. Id., 1912, p. 27; *The influence of mixtures of foodstuffs upon metabolism*. Id., 185; *The cause of the specific dynamic action of protein*. Arch. Int. Med., 1913, 12, 485; *The influence of food on metabolism*. J. Biol. Chem., 1915, xx, 8; *An investigation into the causes of the specific dynamic action of the foodstuffs*. Id., 1915, 20, 555; *The behavior of various intermediary metabolites upon the heat production*. Id., 1921, 49, 453; *The Science of Nutrition*. Philadelphia and London, 1928; *The specific dynamic action*. J. Nutrition, 1931, 3, 519.
- and Chambers. *Specific dynamic action in the normal and phlorrhizined dog*. Internat. Physiol. Congress; in Amer. J. Physiol., 1929, xc, 438.
- Magnus-Levy. *Über die Grösse des respiratorischen Gaswechsels unter dem Einfluss der Nahrungsaufnahme*. Pflügers Archiv., 1894, 55, 1; *The physiology of metabolism*. Anglo-Amer. issue in Noorden. Metabolism and Practical Medicine, Chicago, 1907.
- Mann, Wilhelmj and Bollman. *The specific dynamic action of glycocoll and alanine with special reference to the dehepatized animal*. Amer. J. Physiol., 1927, 81, 496.
- and Boothby. *The respiratory quotient and basal metabolic rate following removal of the liver and injection of glucose*. Id., 1928, 87, 486.

- Mansfeld and Horn. *Über die sogenannte spez-dyn-Wirk. der Nahrungsstoffe. V. Die Wirkung von Nahrungsstoffen auf den Stoffwechsel der isolierten Lunge.* Bioc. Z., 1931, 234, 257
- Mark. *Die Bedeutung der Organspezifität für die spez. dyn. Eiweißwirkung.* Verh. dtsh. Gesell. inn. med., 1929, 523; *Untersuchungen über die Wärmemehrung nach Nahrungseiweiß.* Ergeb. d. inn. Med., 1932, 42, 156.
- Meyer. *Die spezif. dyn. Wirkung des Fleisches beim mit Schilddrüse behandelten Tier (Zugleich ein Beitrag zur Theorie, etc.).* Bioc. Z., 1929, 208, 127; *Über die vermehrte Produktion spezifisch-dynamischer Wärme im Anschluss an Muskular Hochleistungen.* Arbeitsphysiol., 1930, 2, 372.
- Mitchell. *Does the net energy value of food depend upon the purpose for which it is used in the body.* Science, 1927, 66, 289; *The physiological effects of protein.* J. Nutrition, 1928-29, 1, 271.
- and Hamilton. *The Biochemistry of the amino acids.* New York, 1929.
- with the assistance of McClure, Haines, Beadles and Morris. *The Effect of the Amount of feed consumed by cattle on the utilization of its energy content.* J. Agric. Res., 1932, 45, 163.
- Mollgaard. *Fütterungslehre des Milchviehs.* Hannover, 1929; *Über den Begriff des Nährwertes und dessen quantitative bestimmung.* Die Tierernährung, 1929, 1, 44. *Zur Frage der Abhängigkeit des Nährwertes von der Futtermenge.* Id., 1931, 2, 203.
- Mulert. *Über spezifisch-dynamische Wirkung bei intravenos zugeführten Aminosäuren.* Pflügers Archiv., 1929, 221, 599.
- Murlin and Lusk. *The influence of the ingestion of fat.* J. of Biol. Chem., 1915, 22, 15.
- Necheles. *Specific dynamic action of Chinese.* J. Physiol., 1932, 6, 175.
- Neuberg and Hoffman. *Über die Verbrennungswärme des Methyl glyoxals und damit zusammenhängende Fragen.* Bioc. Z., 1932, 252, 440.
- Nicloux. *La combustion de l'alcool chez l'homeotherme.* C. R. Acad. Sci., 1932, 194, 1390; Bull. Soc. Chim. Biol., 1932, 14, 861.
- Nord and Deuel. *The specific dynamic action of glycine given orally and intravenous to normal and to adrenalectomized dogs.* J. Biol. Chem., 1928, lxxx, 115
- Northhaas and Never. *Über die spezifisch dynamische Wirkung and der Künstlich durchgluteten Leber.* Pflügers Archiv, 1930, 224, 527.
- Parnas, Rosenbluth and Wagner. *Ueber den Einfluss der Kohlehydrate auf den Grundumsatz. Nach Versuchen, die an einem Falle besonderer Kohlehydratstoffwechselstörung angestellt wurden.* Z. ges. Expt. Med., 1923, 38, 455.
- Pettenkoffer and Voit. *Respirationsversuche am Hunde bei Hunger und Ausschliesslicher Fettzufuhr.* Z. Biol., 1869, 5, 369; *Über die Zersetzungsvorgänge im Tierkörper bei Fütterung mit Fleisch.* Id., Biol., 1871, 7, 433.
- Plummer, Deuel and Lusk. *The influence of glycyl-glycine upon the respiratory metabolism of the dog.* J. Biol. Chem., 1926, 69, 339.
- Rapport. *The relative specific dynamic action of various proteins* J. Biol. Chem., 1924, 60, 497.
- and Beard. *The effects of protein split-products upon metabolism. I. The fraction extracted by and precipitated in butylalcohol (Fraction I).* J. Biol. Chem., 1927, 73, 285; *II. The individual amino-acids of fraction I of the butyl alcohol extraction and their relation to the specific dynamic action of protein.* Id., p. 299; *The effects of protein split-products upon metabolism. III. Further investigation of the fractionated protein hydrolysates and of amino-acids and their relation to the specific dynamic action of the proteins.* Id., 1928, 80, 413.
- and Katz. *The effect of glycine upon the metabolism of isolated perfused muscle.* Amer. J. Physiol., 1927, 80, 185.
- Reinweinuns Helmut. *Studien über den Mechanismus der spezifisch dynamischen Eiweißwirkung.* Dtsch. Arch. Klin. Med., 1928, 160, 278.
- Richardson and Mason. *The effect of fasting as compared with a diet designed to replace the foodstuffs oxidized during a fast.* J. Biol. Chem., 1923, 57, 587.
- Ringer and Rapport. *The influence of the metabolism of the nucleic acids on heat production.* J. Biol. Chem., 1923, 58, 475.
- Rubner. *Die Gesetze des Energieverbrauches.* Leipzig u. Wien, 1912; *Isodynamic und spezifisch dynamische Wirkung der Nahrungstoffe.* Handb. der norm. und pathol. physiol., 1928, v. 139.
- Schirlitz. *Über die Beziehungen von Blutzuckerhöhe spezifisch-dynamischer Wirkung und Verbrennung bei einer Anzahl von Kohlehydraten.* Bioc. Z., 1927, 183, 23.

- Schlumm and Brechmann. *The specific dynamic action of liver*. Deut. Arch. Klin. Med., 1930, 166, 362.
- Seth and Luck. *The relation between the metabolism and the specific dynamic action of the aminoacids*. Bioc. J., 1925, xix, 366.
- Sherman. *The chemistry of food and nutrition*. New York, 1932.
- Soderstrom, Barr and Du Bois. *The effect of a small breakfast on heat production*. Arch. Int. Med., 1918, 21, 613.
- Spillman and Lang. *The law of diminishing returns*. Chicago, 1924.
- Staehelein. *Versuche über Gaswechsel und Energieverbrauch nach Nahrungsaufnahme*. Z. Klin. Med., 1909, vol. 66.
- Stricker et Bouckaert. *Deperdition calorique pendant l'hyperglycemie experimentale*. C. R. Soc. Biol., 1924, 91, 97.
- Tangle. *Die Arbeit der Nieren und die spezifisch-dynamische Wirkung der Nahrstoffe*. Bioc. Z., 1911, 34, 1.
- Terroine, Trautmann, Bonnet et Jacquot. *L'energie de croissance. III. Rendements energetiques compares dans le developpement des moisissures sur divers aliments organiques et mecanisme de l'action dynamique specifique*. Bull. Soc. Chim. Biol., 1925, 7, 351.
- Terroine et Bonnet. *Le mecanisme de l'action dynamique specifique*. Annal. de Physiol. et Physicochimie biol., 1926, II, 488; *L'influence du taux de la glycemie sur la grandeur des echanges et les problemes de l'action dynamique specifique et de la consommation de luxe*. Arch. di Biol., 1928, 12, 185; *Le mecanisme de l'action specifique. Reflexions sur les observations de M. Aubel et defense de notre doctrine*. Annal. de Physiol. et Physicochimie biol., 1929, v, 268; *Utilisation par l'organisme de l'energie liberee par les oxydations et le probleme de la valeur alimentaire de l'alcool*. Bull. Soc. Chim. Biol., 1929, x, 1223; *Le rendement energetique dans le developpement du Sterigmatocystis nigra sur diverses substances ternaires*. Bull. Soc. Chim. Biol., 1930, xii, 10.
- et Zagami. *Le mecanisme de l'action dynamique specifique de l'alanine, role de l'acide pyruvique et de l'acide lactique*. Bull. Ste' Chim. Biol., 1931, xiii, 326.
- Titus. *Growth and the relation between live weight and feed consumption in the case of white Pekin ducklings*. Poultry Sc., 1928, 7, 254.
- Voit. *Physiologie des Stoffwechsels und der Ernährung*. Hermann. "Handbuch der Physiologie", Leipzig, 1881, 6, 1st part, 209.
- Wang and Hawks. *The Influence of a special breakfast on the basal metabolism of patients with a pathologic condition*. Arch. Int. Med., 1930, 46, 316.
- et al. *The influence of high and low protein diet on the basal metabolism and the chemistry of blood and urine in normal women*. J. Nutrition, 1930, 3, 79.
- Weiss. *Recherches sur l'influence de l'alimentation sur les echanges gazeux de la grenouille*. J. Physiol., et Pathol. Gener., 1910, 12, 457.
- Weiss and Rapport. *The interrelations between certain aminoacids and proteins with reference to their specific dynamic action*. J. Biol. Chem., 1924, 60, 513.
- Wiegner und Ghoneim. *Über die formulierung der jutterwirkung. Ein Beitrag zur theorie der verwertung des unterernährungs—und produktionsfutters auf grund von neuen jutterungsversuchen*. Tierernahrung, 1930, 2, 193. See also Tierernahrung, 1931, 3, 1, in reply to Mollgaards' criticisms in the same journal, 1931, 2, 520.
- Wilhelmj and Bollman. *The specific dynamic action and nitrogen elimination following intravenous administration of various aminoacids*. J. Biol. Chem., 1928, 77, 127.
- and Mann. *The effect of removal of the liver on the specific dynamic action of aminoacids administered intravenously*. Amer. J. Physiol., 1928, 87, 497.
- Wilhelmj and Mann. *The influence of nutrition on the response to certain aminoacids*. Amer. J. Physiol., 1930, 93, 69; *The influence of nutrition of the response to certain aminoacids. II. The effect of fasting followed by diets high in carbohydrates*. Id., 1930, 93, 258.
- and Bollman. *A critical study of certain factors influencing the specific dynamic action of intravenously administered aminoacids and a comparison with oral administration*. Amer. J. Physiol., 1930, xciii, 698; *A study of certain factors concerned in the specific dynamic action of aminoacids administered intravenously and a comparison with oral administration*. Id., 1931, 98, 1.
- Wiley and Newburgh. *The doubtful nature of "Luxus consumption"*. J. Clin. Inv., 1931, 10, 733.

- Williams, Riche and Lusk. *Metabolism of the dog following the ingestion of meat in large quantity.* J. Biol. Chem., 1912, xii, 349.
- Wilson and Lewis. *The rate of absorption of aminoacids from the gastrointestinal tract of the white rat.* J. Biol. Chem., 1929, 84, 511.
- Wishart. *The influence of previous muscular activity and other factors on the basal metabolism.* Quart. J. Med., 1927, 20, 199; *The influence of the protein intake on the basal metabolism.* J. Physiol., 1928, 65, 243.
- Wurmser. *L'energetique et la Biochimie.* Bull. Soc. Chim. Biol., 1923, 5, 506; *oxydations et Reductions.* Paris, 1930.
- Zagami. *Le role des acides ternaires dans l'action dynamique specifique des acides amines et dans le metabolisme intermediaire des glucides.* Bull. Sos. Chimie Biol., 1931, xiii, 343.
- Zuntz. *Einfluss der Geschwindigkeit, der Korpertemperatur und der Uebung auf den Stoffverbrauch bei Ruhe und bei Muskelarbeit.* Arch. ges. Physiol., 1903, 95, 192. *Die Bedeutung der verdauungsarbeit im gesamtstoffwechsel der menschen und der Tiere.* Naturw. Rundschau, 1906, 21, No. 38; *Zur erklarung der "spezifisch-dynamischen wirkung" der Eiweisstoffe.* Zentralbl. Physiol., 1908, 22, 61; *Verdauungsarbeit und spez-dynamische Wirkung der Nahrungsmittel,* Med. Klinik, 1910.
- and von Mering. *Inwiefern beeinflusst Nahrungszufuhr die tierischen Oxydationsprozesse.* Pflug. Arch., 1883, 23, 173; Id., 1877, 15, 634.