

THE INFLUENCE OF ENVIRONMENTAL TEMPERATURE
ON THE UTILIZATION OF FOOD ENERGY IN
BABY CHICKS*

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INTRODUCTION

The influence of the environmental temperature on the vital functions of poikilothermic organisms has been extensively investigated. Van't Hoff's rule for the relation of temperature and velocity of chemical action has been applied to physiological problems, for example, the development of sea urchin eggs by Abegg and to photosynthesis by Matthaei (Verworn, 1922). Crozier (1924-25) and coworkers have demonstrated that Arrhenius' equation for the velocity of irreversible chemical processes as functions of temperature expresses very well the influence of environmental temperature on a great number and variety of vital processes in organisms or parts of organisms. Stier (1932-33) has shown that one may consider the inheritance of distinct temperature characteristics for the frequency of respiratory movements even in mammals at least during a time when the temperature regulation is not yet developed as in new born mice.

Temperature optima have been observed for the development of various poikilotherm organisms, as for *B. tuberculosis* 37-38°C. by Koch. Surface yeast according to J. Albauer grows fastest at 33-34°C.; for sediment yeast Pederson found maximum growth rate at 29°C. (Mayer, 1927).

The main object of the investigation reported in this paper was to

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study how the environmental temperature affects growth rate, food consumption, and the conversion of food to body substance in homoiotherms where the environmental temperature has little if any direct effect on the temperature of the majority of body cells.

The influence of the environmental temperature on the metabolism of homoiotherms has been studied mainly on fasting animals to eliminate influences of food intake on the result of the experiment.

These investigations point to the existence of a certain critical environmental temperature below which a cooling of the environment causes an increase in metabolism and above which the metabolism is practically independent of changes in the environmental temperature.

The broken line, *abc*, on a temperature-metabolism chart (see Fig. 1) illustrating this behavior of homoiotherms may be interpreted as a result of two curves which in the first approximation are straight lines, one (inclined) representing the heat requirement for maintaining the animal's body temperature at a constant level, and the other (horizontal) indicating the minimum heat production of the animal. The critical temperature T_{c_1} is then defined as the temperature at which the two lines coincide. If the animal is fed, the level of the minimal heat production is raised for the amount of the heat increment, or the specific dynamic action of that food, C_m and C_p . This increase in the minimal heat production lowers the critical temperature to T_{c_2} for maintenance and to T_{c_3} for full feeding.

The influence of variations in temperature on the animal receiving a certain food was studied on dogs by Rubner (1902), who condensed the results of this investigation to his so called compensation theory. According to this theory, the metabolism below the critical temperature for the full fed animal T_{c_3} is not affected by food intake (no specific dynamic action of the food). Above the critical temperature for fasting, T_{c_1} , the specific dynamic action of the food is constant; *i.e.*, independent of the changes in the environmental temperature. In the region between these two critical temperatures, the specific dynamic action increases in proportion to the increase in temperature. Rubner's compensation theory seems not to have been given much attention in experiments. In general, the investigators were careful only to keep their animals above the critical temperature in order to obtain results independent of temperature changes.

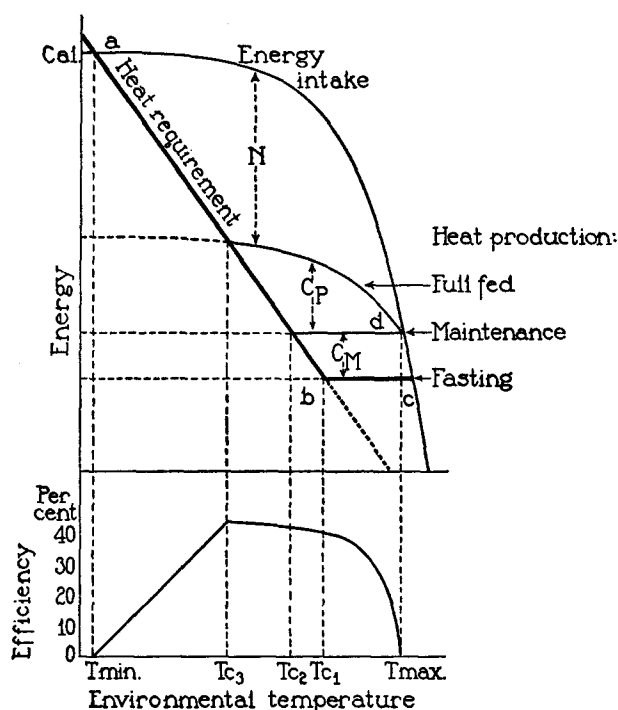


FIG. 1. Scheme of energy transformations in homoiotherms as a function of environmental temperature. The inclined straight line marks the heat requirement; *i.e.*, the amount of heat which would be necessary to maintain the animal's body temperature if the animal were an ordinary thermostat. Since the radiation depends on the difference of the 4th powers of temperatures this line is actually a curve. For small differences in temperature, however, it does not deviate considerably from a straight line.

Below the critical temperature, T_{c_1} , the heat production of the fasting animals follows the line of the heat requirement; above that temperature it is independent of further changes in temperature (minimum heat production). At high environmental temperatures the heat production rises again with rising temperature. This effect is omitted in the scheme.

C_m indicates the specific dynamic action of the food for maintenance which brings the heat production to a higher level and lowers the critical temperature to T_{c_2} .

C_p illustrates the specific dynamic action of the production food calculated to be 33 per cent of the energy intake above maintenance.

The difference between the energy taken in and the heat produced is the net energy N .

The net energy in per cent of the total food energy is the efficiency. It is maximum at T_{c_3} ; *i.e.*, at the critical temperature for the full fed animals.

Our study was undertaken to investigate the influence of temperature changes on the energy transformation of fed animals including the range below the critical temperature which has commonly been avoided. Instead of giving definite rations, as has been done in most former experiments, we let the animal itself determine the amount of food intake. In this way, we studied the appetite in relation to the environmental temperature, growth rates, and energy utilization, as an important variable which determines in a great many cases the actual level of energy transformation in animals.

From our own experience, we know that our appetite is greater in cold than in hot weather.¹ Thus, if enough food is available, the increased requirement for temperature regulation at lower environmental temperatures is paralleled by an increased energy intake. This parallelism is, however, not complete. The lower the environmental temperature, the higher is the heat requirement for temperature regulation. The energy intake to the contrary cannot increase indefinitely because the capacity of animals for eating, digesting, and absorbing food is limited. It is, therefore, to be expected that at sufficiently low environmental temperatures the energy intake of the animal can no longer keep pace with its heat requirement and the animal starves to death even though it eats to capacity. The temperature at which the curve of the heat requirement and the curve of intake of metabolizable energy coincide (point *a* in Fig. 1) is the minimum temperature ($T_{min.}$) under which the animal is able to maintain its life continuously. At this temperature, naturally, no energy will be available for production of body substance. Thus the net energy² and consequently the total efficiency of the animal as a converter of food energy will be zero. The production of body substance will also be zero at extremely high environmental temperatures when the appetite is decreased to such an extent that the energy intake covers only the minimal heat production for maintenance (*d* in Fig. 1). This temperature is the maximal temperature ($T_{max.}$) which an animal can survive continuously.

Between the two extreme temperatures at which no production can

¹ The contrary is true for grasshoppers which, in an experiment by Parker (1930), consumed at 37°C., 2.5 times as much food as at 27°C.

² Net energy = heat of combustion of produced body substance.

take place because too much energy is lost at one and too little is taken in at the other, there should be a temperature at which the production is maximum, and one at which the total efficiency; *i.e.*, the quotient of net energy to total energy intake, is maximum. In our schematic graph, Fig. 1, they are both at T_{c_3} the critical temperature for maximal food intake.

Method

From a hatch of White Leghorn chicks 5 days of age, five individuals were selected and banded as the experimental group, and eight as the control group. Sex did not appreciably affect the results since the number of male and female chicks in each of our trials happened to be almost equal as shown by investigation several weeks after the trial when the sex characteristics began to develop. Also in these young birds the differences of sex with relation to growth seem not to be considerable according to Jull and Titus (1928) who found that for the first 6 or 8 weeks the female chicks weighed practically the same as the males. The controls were kept in a brooder which was so constructed that the chicks could stay at a temperature of 35°C. or go into an outer compartment at room temperature as they chose. This choice was somewhat influenced by the fact that the food was kept in the outer compartment. The experimental chicks were kept in the respiration chamber at constant temperature and humidity, except for about 15 minutes in the morning and evening, which time was required for obtaining the individual weights, changing the food and water, and collecting the excrement.

Each experiment for one level of temperature lasted 9 days and was followed by the determination of the fasting metabolism. The experiments at the various temperatures were carried out in the following sequence: 38°, 27°, 40°, 32°, 21°, 40°C.

The food was considered qualitatively adequate for every requirement.³ Portions of 150 gm. were weighed and stored in glass jars before the trial started. The food was given every morning in a food box which was constructed to prevent

³ The food was prepared in pellet form according to the following recipe:

Mix 25 parts of ground whole wheat,
25 parts of ground whole yellow corn,
25 parts of ground whole barley,
15 parts of fish scrap with 65 per cent protein,
5 parts of dry skim milk,
5 parts of ground bone.

To 100 parts of this mixture add:

2 parts of pulverized lime stone (96 per cent CaCO_3),
 $\frac{1}{2}$ part of salt (NaCl),
1 part of cod liver oil.

the birds from contaminating the food by excrement. The amount of food given was abundant, intake being limited only by the appetite of the chicks. The remaining food was taken out in the evening and put into a drying oven at 105°C. for the moisture determination so that the amount of the dry matter eaten by the group was known for each day. No food was given during the night.

The excreta were removed every day from the pan below a false floor of chicken wire, dried at 105°C., and weighed before cold. The dried excreta for the whole period of 10 days were stored in a glass jar and a composite sample was analyzed.

Food and excreta were analyzed for N according to Kjeldahl and for C by the method of wet combustion with potassium dichromate. The heat of combustion was determined in an Emerson fuel calorimeter.

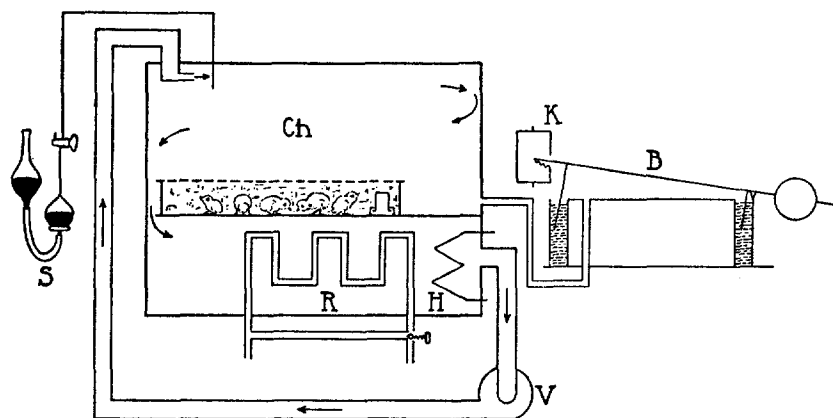


FIG. 2. Climatic cabinet. *ch*, chamber; *R*, refrigerator coil; *H*, electric heater; *V*, air circulation; *B*, pressure regulator; *K*, kymograph drum; *S*, sample for gas analysis.

The respiratory exchange of the experimental chicks was determined in a closed chamber constructed as a climatic cabinet (Fig. 2). This cabinet is a horizontal metal cylinder 91 cm. inside diameter and 122 cm. inside length covered with cork for insulation. Five electrical heaters (*H*), each controlled by a separate outside switch, are installed in the chamber, giving a total heating power of 2250 watts. One of the 500 watt units is a control element operated by an automatic temperature regulator. A system of brine coils (*R*) for the regulation of the humidity is mounted in the lower part of the chamber. The flow of brine through these coils is under the control of a wet bulb air thermometer inside the chamber which influences a diaphragm valve, opening and closing a by-pass in the brine duct. A fan (*V*) circulates the air inside the chamber over the cooling and heating systems. A heavy round door with a thick walled glass window is mounted on a hinge at the front of the chamber and may be screwed against a rubber gasket for an air-tight closure.

The air-conditioning devices produce regulatory oscillations of the temperature and humidity inside the chamber, which would cause resultant fluctuations in air pressure if the volume remained constant. If there is the slightest leakage these variations in pressure tend to cause an exchange between the air in the chamber and the air outside. These changes in pressure are practically avoided by a regulator (*B*) providing a calibrated buffer volume.

A sample of the air in the chamber is taken at the start and at the end of a period. This gas sample is analyzed for CO₂ and O₂ in a modified Haldane apparatus (Kleiber, 1933 *b*).

The volume of the chamber has been determined by introducing volumetrically measured amounts of CO₂ from a bomb and determining the difference in CO₂ concentration thus effected; it has also been measured by burning known amounts of ethyl alcohol in the chamber and determining the increase in CO₂ concentration due to this combustion. In five tests by introduction of CO₂ gas the volume was found to be 890 ± 13.5 liters. In seven tests with combustion of alcohol, the determined volume was 898 ± 11.9 liters.

RESULTS

(a) *Influence of Temperature on the Growth Rate of Baby Chicks*

The chicks were weighed individually each morning after having been 12 hours without food, and every evening. The average morning weight for all experimental groups at the start of the experiment was 55 gm. with extremes from 53 to 58 gm. At the end of the experiment, the body weight of the 15 days old chicks differed considerably according to the temperature at which they had been kept, ranging from 79 gm. each for the group kept at 40°C. to 99 gm. each for the group kept at 21°C.

In Fig. 3 the average growth rate for 6 to 15 days of age is plotted against the environmental temperature. The growth rate of all controls for which, of course, the abscissa has no meaning, is averaged and drawn as a dotted line.⁴ From the value for the growth rate of the experimental chicks the solid curve is interpolated. The curve shows a tendency to reach a maximum which, however, would be at a temperature lower than 21°C.

The curve of the growth rate of the experimental chicks reaches the

⁴ The growth rate of the controls simulates a relation to the temperature at which the experimental chicks were kept. The dot and dash line in Fig. 3 is the result of interpolation by the method of least squares. This line used as a basis of comparison leads, however, to the same conclusions as the line which expresses the average of the controls.

average level of the growth rate of the controls at a temperature between 32°C. and 38°C.

At an environmental temperature above 32°C., the experimental chicks had a lower rate of growth than the corresponding controls. Below this temperature the growth was the more stimulated the lower the environmental temperature.

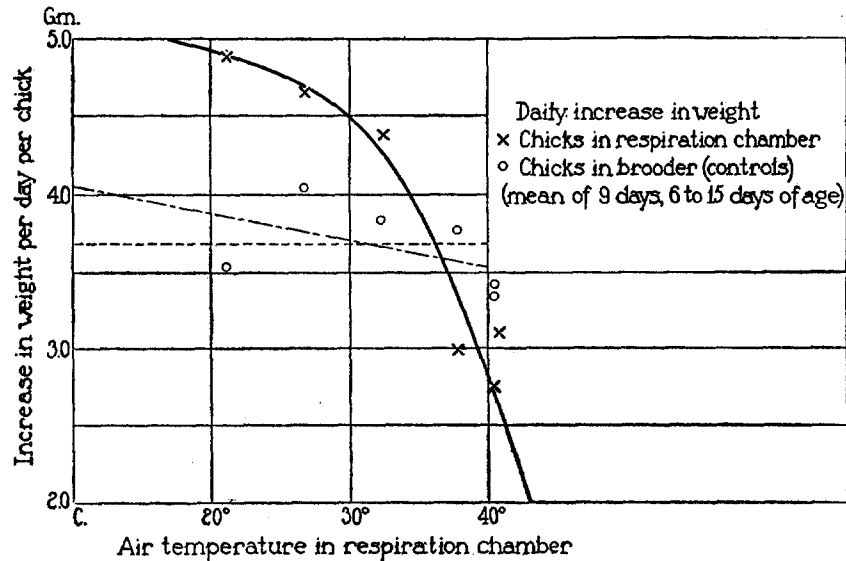


FIG. 3. Growth rate and air temperature.

Since the daily increase in weight in growing animals depends on the weight itself, the relative rate of growth is more satisfactory than the absolute rate for comparing the velocity of growth in animals of different size.

The relative rate of growth for our chicks has been calculated according to the definition given by Brody (1926-27, p. 641) for the accelerating phase of growth:

$$\frac{dW}{dt} = k \cdot W$$

The meaning of the terms in our calculation was:

- W = body weight in grams.
- t = time in days.
- k = relative rate of growth.

The integrated form of the function

$$k = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} = 2.30259 \frac{\log W_2 - \log W_1}{t_2 - t_1}$$

has been used, basing the calculation on the weight at the age of 5 days, the average of the weights at 10 and 11 days, and the weight at 15 days of age.

Table I shows the results of this calculation. The relative growth rate is greater the lower the environmental temperature. In all but one case (38°C.) the relative growth rate is higher in the second period (10.5 to 15 days of age), than in the first one. This behavior is also

TABLE I
Relative Growth Rate of Experimental Chicks According to Brody's Formula

Air temperature °C.	Per cent growth per day: (100k) during the period of age of:		
	6-10.5 days	10.5-15 days	6-15 days
21	6.2	6.9	6.5
27	5.7	6.6	6.2
32	5.8	6.4	6.1
38	4.9	4.4	4.6
40	3.8	4.6	4.2
40	3.5	5.5	4.5

found in the controls except that the controls for one trial out of 6 had a slower relative rate of growth in the second period. All other chicks showed an acceleration of growth with increasing age greater than that which is to be expected according to the assumption that the rate of growth is proportional to the weight. The average relative rate of growth for the control groups was 4.78 per cent per day of the second period (10.5 to 15 days old) and 5.17 per day of the period from 6 to 15 days of age. Our experiments thus confirm the statement of Brody (1926-27, p. 646) that "fowl grows at 5 per cent per day up to 3 weeks."

(b) *Influence of Temperature on Food Consumption and Excretion Availability*

The increased rate of growth with the decrease in the temperature of the surrounding air is paralleled by an increased appetite. Table II

contains the mean results of the food consumption per chick for the first and second period as well as for the entire time of the experiment.

Since the food consumption depends on the body size and the average weights are considerably different, it is advisable, for the comparison of the appetite at different temperatures, to reduce the data to comparable body size. The $3/4$ power of body weight has been found to be most suitable as a basis for comparison of the metabolism of large and small animals (Kleiber, 1932). There is a close relation

TABLE II
Food Consumption, Excretion, and Availability at Various Temperatures
Grams Dry Matter per Day per Chick

Age	Air temperature, °C.....	21	27	32	38	40	40
<i>days</i>							
6-10	Food, gm.	11.88	11.22	10.70	8.16	7.48	6.54
	Excretion, gm.	4.72	4.34	3.95	2.97	2.78	2.52
	Available, gm.	7.16	6.88	6.75	5.19	4.70	4.03
	Availability, per cent.	60.3	61.3	63.1	63.7	62.8	61.3
11-15	Food, gm.	18.18	15.38	12.27	9.30	8.40	9.36
	Excretion, gm.	7.14	5.86	4.55	3.33	3.12	3.44
	Available, gm.	11.04	9.52	7.72	5.97	5.28	5.92
	Availability, per cent.	60.7	61.9	62.9	64.2	62.9	63.3
6-15	Food, gm.	15.03	13.30	11.69	8.73	7.94	7.95
	Excretion, gm.	5.93	5.10	4.32	3.15	2.95	2.98
	Available, gm.	9.10	8.20	7.37	5.58	4.99	4.97
	Availability, per cent.	60.6	61.7	63.0	64.0	62.8	62.5

between metabolism and food consumption (Kleiber, 1933 *a*), therefore the $3/4$ power of body weight should also be a suitable basis for comparing levels of food consumption.

The food consumption per $W^{3/4}$ in these trials is very nearly a linear function of the air temperature. The relation between F_t , representing the intake of grams dry matter per unit of the $3/4$ power of the body weight in kilos and the environmental temperature in degrees Centigrade may be expressed as follows:

$$F_t = 81.0 + 2.15 (32.2 - t) \text{ for temperature below } 32.2^\circ\text{C.}$$

$$F_t = 81.0 + 2.24 (32.2 - t) \text{ for temperature above } 32.2^\circ\text{C.}$$

It is surprising that this proportionality between temperature and food consumption should exist over such a considerable range of temperature. Since the maximum amount of food which can be taken in and digested per day must be limited, it was to be expected that toward the lower temperatures, the curve of the food consumption should approach asymptotically this maximal food capacity (see Fig. 1). More rapid decrease in food consumption with increased air temperatures above 38°C. was also expected. It seems to follow from the

TABLE III
Liters CO₂ Produced per Day by Baby Chicks

Air temperature, °C.....		21	27	32	38	40	40
(a) Per chick							
1st period.....	6-10 days old	5.28	4.03	3.62	2.98	2.73	2.46
2nd period.....	11-15 days old	7.22	5.95	4.57	3.64	3.10	3.38
Total trial.....	6-15 days old	6.25	5.00	4.21	3.35	2.92	2.98
(b) Per kg. body weight							
1st period.....	6-10 days old	85.0	63.3	56.4	50.8	47.6	44.3
2nd period.....	11-15 days old	83.3	68.5	55.5	50.0	43.6	46.6
Total trial.....	6-15 days old	84.1	65.9	55.8	50.4	45.6	45.6
(c) Per kg. ^{3/4} of weight ^{3/4}							
1st period.....	6-10 days old	42.4	31.8	28.5	25.1	23.3	21.5
2nd period.....	11-15 days old	44.4	37.3	29.8	26.0	22.6	24.2
Total trial.....	6-15 days old	43.4	34.5	29.3	25.6	22.9	23.0

results of these experiments that at extremely high or low air temperatures, the food intake as a function of this temperature must change abruptly.

The amount of dry matter consumed daily per kilo of body weight ranges from 120 gm. at 40°C. to 200 gm. at 21°C. If it is assumed that the body of the chick contains 30 per cent dry matter, it follows that at a temperature of 21°C. the chick eats daily 2/3 of the amount of dry matter in its own body. The increase in body weight per gram dry matter of food consumed shows a maximum of 0.375 gm. gain per gm. food at 32°C. dropping to 0.325 gm. at 21°C. and 0.324 gm. at 40°C.

The excreta of the chicks contain the non-digested part of the food as well as the secretion of the urinary system. They are therefore not comparable to the feces of mammals. One manifestation of this difference between the two kinds of excreta is the fact that the energy content as well as the C content per gram dry matter in the chick excreta are lower than the corresponding contents of the food. Calculated per 100 gm. dry matter, the food contained 41.2 gm. C, while the C content of the excreta varied from 34.3 gm. to 38.0 gm.

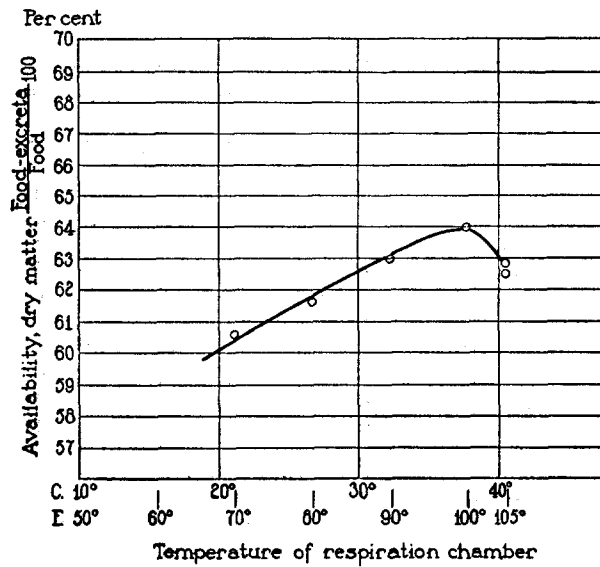


FIG. 4. Availability and air temperature.

with an average of 36.3 gm. The corresponding energy content of the feed was 432 Cal. while the excreta contained an average of only 371 Cal. with variations from 361 to 386 Cal. In herbivorous mammals, to the contrary, the energy and C are more concentrated in the feces than in the food, mostly due to the fact that the lignin, which has a high concentration of energy and carbon, is practically non-digestible. The nitrogen, on the other hand, is increased in the excreta of the chicks (4.15 gm. N per 100 gm. dry matter as compared to 2.89 gm. N per 100 gm. dry matter in the food).

We do not attempt to determine digestibility in these chick trials,

but use for comparison a conception which is better adapted to nutrition work with birds and to which we give the name *availability* of the food. If per 100 gm. dry matter of food eaten, 40 gm. are excreted as feces and urine, 60 gm. dry matter remain *available* for combustion or for the production of body substance, then the availability of the dry matter is 60 per cent. The availability is given in Table II. The results for the first and second periods of each single trial are in very close agreement. The mean availability for both periods is plotted against the environmental temperature in Fig. 4.

At an air temperature of 38°C., the availability is 64 per cent, the maximum in our experiments. With decreasing temperature it drops at the average rate of 0.12 per cent per degree drop in temperature.

TABLE IV
Respiratory Quotient of Full Fed Baby Chicks at Different Temperatures

Air temperature, °C.	21		27		32		38		40		40	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
<i>days</i>												
6-10	0.994	0.914	1.036	0.940	1.053	0.965	1.040	0.998	1.004	0.869	0.984	0.865
11-15	1.011	0.936	1.157	0.916	1.051	0.906	1.039	0.957	1.061	0.911	1.070	0.966
6-15	1.002	0.925	1.080	0.928	1.052	1.928	1.040	0.977	1.032	0.890	1.032	0.915
Day and night	0.971		1.018		0.990		1.012		0.966		0.979	

At temperatures above 38°C. the availability is also decreased to an average of 62.7 per cent at 40°C. It remains to be studied whether the drop in the availability with decreasing temperatures is the result of the increasing amount of food consumed, which would parallel unpublished results obtained by the senior author on rabbits and sheep, which show a decrease in the digestibility with an increase in food consumption.

(c) *Influence of the Environmental Temperature on the Respiratory Exchange*

Like other homoiotherms, the baby chicks respond to a lowering of the environmental temperature with an increased metabolism. This behavior is clearly shown in Table III.

At 40°C. one chick of 6 to 15 days of age produced a daily average of 2.95 liters CO₂. With every drop in temperature, without exception, the average daily CO₂ production was increased. At 21°C. the respiratory exchange was twice as high as that at 40°C., reaching a level of 6.25 liters CO₂. The same behavior is shown if the daily CO₂ production is calculated separately for the first and second periods of the experiment. Essentially the same result is obtained if the CO₂ production is calculated per kilo of body weight. It ranges, for the total period (6 to 15 days of age), from 45.6 liters CO₂ per kilo at 40°C. to 84.1 liters CO₂ per kilo at 21°C., where the daily loss of 165 gm. of CO₂ per kilo of body weight amounts to more than 50 per cent of the dry matter contained in the body of the chick.

Calculated to the 3/4 power of the body weight, the daily CO₂ production of the chicks increased from 23 liters CO₂ per kilo^{3/4} at 40°C. to 43.4 liters per kilo^{3/4} at 21°C. At 38°C. the chicks produced daily 25.6 liters CO₂ per kilo^{3/4}.

In four beef heifers in another experiment, the daily CO₂ production at full feed amounted to 24.2 liters per unit of the 3/4 power of the body weight. Since the temperature of 20°C., at which the heifers were kept, corresponds better, physiologically, to 38°C. for baby chicks than to a lower temperature, the comparison seems to indicate that the respiratory exchange of our baby chicks was in agreement with the rule that the metabolism per unit of the 3/4 power of the body weight of warm blooded animals is independent of body size.

During the experiment, the daily CO₂ production per unit of the 3/4 power of the body weight increased at an average daily rate of 1.3 ± 0.5 per cent of the mean CO₂ production for the total period of 9 days.

This increase in the respiratory exchange with increasing age is somewhat comparable to the increase in metabolism of children. According to the measurements of Benedict and Talbot (1921) the basal metabolism of boys increases during the period of 6 months to 18 months of age 14 per cent of the value of the age of 1 year. The corresponding increase for girls is 15 per cent. If it can be assumed that the metabolism of the chicks at full food is a certain multiple of the basal metabolism, then it would follow that the per cent increase in metabolism in children in 1 year is of the same magnitude as that of the baby chicks in 12 days. The ratio of 1 year human life to 12 days chick life seems to be of the same order for sex maturity.

The *respiratory quotient* varies little for different temperatures, as shown in Table IV. There seems to be a tendency for the R.Q. to be

lower at the extremely low and high air temperatures. Much more marked than the variation at different temperatures is the variation in R.Q. between day and night. It seems natural to explain this difference by the fact that the chicks ate no food during the night. The average R.Q. of all the day runs is 1.033 ± 0.010 , and the average of the night runs 0.924 ± 0.010 . The fact that the R.Q. during the day is higher than unity may be related to an intensive production of body fat from carbohydrates. During the night, the chicks were without food and their lower R.Q. indicated a decrease in fat production. The metabolism of the birds during the night, however, was far from fasting metabolism, since 24 to 36 hours after the last food the chicks had a respiratory quotient of 0.734 ± 0.009 (Table VII).

(d) N, C, and Energy Balances

For the sake of economy of space the twenty-seven tables giving the N, C, and energy balances are not printed. From the composition of the food and feces, and the amount of dry matter eaten and excreted daily, the amount of N, C, and energy taken in and excreted daily is calculated. The difference between the intake and excretion is the amount of N, C, and energy which is available for combustion or production of body substance. The amount of C lost as CO_2 is calculated from the result of the respiration trial. For each liter CO_2 given off by the animal, 0.5359 gm. C is subtracted from the available C. The rest is the carbon stored in the body (net). The amount of protein gained is calculated by multiplying the figure for the available N by 6.25. The amount of C contained in the stored protein is 3.25 times the amount of available N. The amount of C in protein is subtracted from the total amount of C stored, and the rest is the amount of C in the produced body fat, which contains 76.5 per cent C. The net energy is obtained as the sum of the heat of combustion of the stored protein (1 gm. protein = 5.7 Cal.)⁵ and the stored fat (1 gm. body fat = 9.5 Cal.). The heat production of the animal is calculated as the difference between the available energy and the net energy.

The heat production of the birds was larger in the second period of the trial, corresponding to the increased respiratory exchange which has already been discussed. The influence of the environmental tem-

⁵ In this paper the energy is expressed throughout in kilogram calories.

perature on the heat production is very consistent. In both periods, the heat production of the animal was greater the lower the air temperature. Table V gives the summary of the results on energy metabolism obtained per chick for the total duration of the experiment.

As the temperature is increased above 32°C. the heat production is decreased at the same rate as the food consumption. At the extremely low temperatures, the food consumption seems no longer to keep pace with the increase in metabolism. At 21°C. the food intake was increased to 128 per cent, the available energy to 121 per cent, the heat production, however, to 153 per cent of the value at 32°C. This observation seems to confirm the hypothesis that with lower tem-

TABLE V
Energy Transformation in Full Fed Baby Chicks for the Period of 6 to 15 Days of Age

Air temperature, °C.....	21	27	32	38	40	40
Average body weight, gm.....	74.2	75.4	71.7	65.1	64.0	64.5
Average units of $W^{3/4}$, kg. ^{3/4}	0.142	0.144	0.138	0.129	0.127	0.128
Energy in food per day per chick, Cal.	65.2	56.6	51.1	37.5	34.1	34.5
Energy in excreta per day per chick, Cal.	22.9	18.8	16.1	11.4	10.8	11.1
Available energy per day per chick, Cal.	42.3	37.8	35.0	26.1	23.3	23.4
Heat production per day per chick, Cal.	35.4	27.4	23.2	17.4	15.9	17.4
Net energy per day per chick, Cal.	6.9	10.4	11.8	8.7	7.4	6.0

perature, the heat production tends to approach the energy intake, since the latter is naturally limited.

The net energy shows a maximum of 11.8 Cal. per chick per day at 32°C. decreasing to 6.9 Cal. at 21°C. and an average in two trials of 6.7 Cal. at 40°C. The energy transformation of the baby chicks as a function of the air temperature is illustrated in Fig. 5. In order to avoid in this graph possible influences of body size, the energy exchange is calculated per unit of the 3/4 power of body weight. The energy intake appears to decrease in proportion to the increase in the air temperature at a rate of -10.4 Cal. per °C. The available energy, however, shows the tendency to reach a maximum at low environmental temperatures. It seems to follow from these two curves that in baby chicks the expected limitation of energy intake is a question of the digesting or absorbing power of the intestinal tract rather than of the

appetite. The curve for the heat production of the animals is bent in the opposite direction to that for the available energy. By extrapolation of these two curves a point of coincidence is found between 15°C. and 20°C. At this temperature the animal would lose as much energy in the form of heat as it can make available from the food; therefore, no body substance could be produced. The net energy at this low temperature would consequently be zero. It reaches its maximum at 32°C. and drops as the temperature of the environment

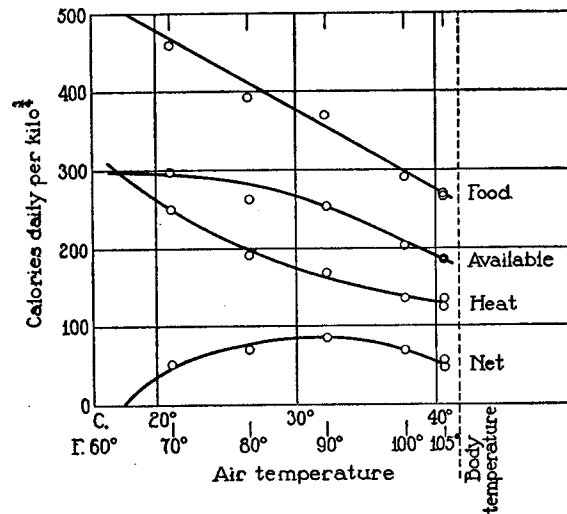


FIG. 5. Energy exchange and air temperature.

approaches the body temperature which, according to several measurements after the trial, was 41.7°C.

(e) *Composition and Energy Content of the Gain in Body Substance*

The energy metabolism of our chicks has been calculated on the basis of the C and N balances assuming that the main organic constituents of the gain in body substance are protein and fat. Table VI shows the influence of environmental temperature on the daily production of these two groups of compounds. The storage of protein was higher, as was the gain in body weight, the lower the outside temperature. The production of body fat, on the other hand, had a maximum at 32°C. air temperature, falling almost to zero as the temperature de-

creased to 21°C. and also dropping considerably with increasing temperatures above 32°C. The daily gain in net energy by no means paralleled the growth rate (in terms of body weight). At 21°C. air temperature with the highest gain in weight, the storage of net energy was next to the lowest obtained, the maximum being at 32°C. This result shows that the body weight is no general criterion for the effect of food on energy storage in the animal.

The question may be raised whether the gain in weight or the gain in energy is a more adequate expression for growth. If the deposition of body protein is considered an important characteristic of growth,

TABLE VI
Composition and Energy Content of the Daily Gain of Baby Chicks at Various Environmental Temperatures
Period: 6 to 15 Days of Age

Air temperature, °C.....	21	27	32	38	40	40
Daily gain in body weight, gm.....	4.88	4.64	4.39	2.97	2.74	3.09
Daily production of body protein, gm.....	1.10	1.08	0.97	0.79	0.69	0.67
Daily production of body fat, gm.....	0.06	0.44	0.67	0.44	0.37	0.24
Daily net energy, Cal.....	6.9	10.4	11.8	8.7	7.4	6.0
Per gm. increase in body weight:						
Body protein, gm.....	0.225	0.233	0.221	0.266	0.252	0.217
Body fat, gm.....	0.012	0.095	0.153	0.148	0.135	0.078
Inorganic matter (mostly water), gm.....	0.763	0.672	0.626	0.586	0.613	0.705
Energy, Cal.....	1.41	2.24	2.69	2.93	2.70	1.94

then the gain in weight would be preferred to the gain in energy. It is seen in Table VI that the gain in protein changes only from 0.22 gm. to 0.27 gm. per gm. increase in body weight. No influence of the environmental temperature on the protein content of the gain in body weight seems to exist. Such an influence on the gain in body fat per unit of gain in weight is, however, very marked. The greatest gain of fat was made at a temperature of 32°C., 0.153 gm. fat being deposited per gram increase in weight. The increase in weight at 21°C. contained only 1 per cent fat and consequently a higher water content (76.3 per cent compared with 58.6 per cent at 38°C.). The gain at 38°C. had the highest concentration of energy, 2.93 Cal. per gm. of increase in weight, compared to 1.41 Cal. at 21°C.

(f) *Basal Metabolism*

The basal metabolism of the chicks has been determined at the end of each trial, starting in the evening when the chicks had been without food for 24 hours, and ending the following morning. The results of these experiments, calculated to 24 hours are given in Table VII. The heat production is calculated from the oxygen consumption, using a standard of 4.7 Cal. per liter of oxygen consumed. The basal heat production is increased as the outside temperature is decreased. It is to be expected in warm blooded animals that above a certain so called critical temperature of the environment, the metabolism is independent of changes in this temperature. No evidence of such a critical

TABLE VII
Basal Metabolism of Baby Chicks at Various Temperatures at 16 Days of Age

Air temperature	No. of experiment	Body weight W	$W^{3/4}$ kg. ^{3/4}	Daily respiratory exchange per chick		R.Q. $\left(\frac{\text{CO}_2}{\text{O}_2}\right)$	Daily heat production		
				CO ₂	O ₂		Per chick	Per kg.	Per $W^{3/4}$
°C.		gm.		liters	liters		cal.	cal.	cal.
21	11	85.6	0.158	3.28	4.32	0.76	20.3	237	128
27	7	88.6	0.162	2.50	3.52	0.71	16.5	186	102
32	9	84.3	0.156	2.14	3.01	0.71	14.1	167	90
38	6	73.1	0.140	1.81	2.48	0.73	11.7	160	83
40	8	73.9	0.142	1.12	1.53	0.73	7.2	98	51
40	12	74.4	0.142	1.50	2.11	0.71	9.9	133	70

temperature was found. Considering the relatively large variations, the number of experiments is not adequate to conclude that no such critical temperature exists for the metabolism of these young birds. If a critical temperature exists it is safe to state on the basis of our trials that it is considerably higher for baby chicks than adult chickens which Mitchell and Haines (1927 *a*) found to be 16.7°C.

The average figure for the basal metabolism of our chicks at 38°C. and 40°C. is 68 Cal. per kilo^{3/4}. From the measurements of Mitchell and Haines (1927 *b*) it follows that the basal metabolism of their mature hens amounted to an average of 64 Cal. per kilo^{3/4}. The corresponding figures per unit of weight are 130 Cal. per kilo for the baby chicks and 54 Cal. per kilo for the mature hens. This comparison shows that the metabolism of fowls of different size is more closely

related to the unit of the $\frac{3}{4}$ power of the weight than to the unit of weight itself, which is in accordance with the results in other homoiotherms as discussed in an earlier paper (Kleiber, 1932).

(g) *The Heat Increment of the Feed at Various Temperatures*

From the figures for the basal metabolism and the metabolism at full feed the heat increment (Armsby) or specific dynamic action (Rubner) of the feed has been calculated in Table VIII. For this calculation, it had to be considered that during the test for the basal metabolism the birds were heavier and older than in the average during the period of full feed. In order to eliminate the discrepancies in

TABLE VIII
Heat Increment of the Food of Baby Chicks at Various Environmental Temperatures

Temperature of air, °C.....	21	27	32	38	40	40
Daily basal heat production per kg. ^{3/4} calculated to the age of 10.5 days, Cal.	121	97	85	78	48	66
Daily heat production at full feed, per kg. ^{3/4} , Cal. . .	249	190	168	135	125	136
Daily heat increment of full feed per kg. ^{3/4} , Cal. . .	128	93	83	57	77	70
Daily available energy in food per kg. ^{3/4} , Cal.	298	262	254	202	183	183
Heat increment per 100 Cal. available. Energy at full feed, <i>per cent.</i>	43	36	33	28	42	38

weight, the heat production in both cases is calculated per unit of the $\frac{3}{4}$ power of the body weight.⁶

For making the basal metabolism determined at the age of 16 days comparable to the metabolism at full feed with an average age of 10.5 days, it has been assumed that during the period studied the basal metabolism in these birds increased 1 per cent of the average for each day increase in age as found for the metabolism at full feed (see page 714). This assumption seems to be justified because the total energy intake for very different animals seems to approximate the same mul-

⁶ For the sake of simplicity, the average metabolism per chick as given in Table V has been divided by the $\frac{3}{4}$ power of the average weight. The result does not differ considerably from that obtained by calculating the metabolism for each day to the unit of the $\frac{3}{4}$ power of the corresponding weight and then taking the average.

tion of the basal metabolism (Kleiber, 1933*a*), and the metabolism at full feed is closely related to the energy intake. Thus a theoretical basal metabolism for the age of 10.5 days has been calculated on the basis of the equation:

$$B_{10.5} \times (1 + 0.01 \times 5.5) = B_{16}$$

where $B_{10.5}$ = basal metabolism at the age of 10.5 days,

and B_{16} = basal metabolism at the age of 16 days.

According to Rubner's compensating theory it is to be expected that at lower environmental temperatures the specific dynamic action is decreased because the extra heat developed after food consumption is used for maintaining the body temperature and saves a corresponding amount of food or body substance which would have been used as fuel. Consequently, the gap between basal metabolism and metabolism at full food should become smaller as the outside temperature decreases and if it falls below the critical temperatures for maximal food intake, the heat production should become independent of the amount of food consumed, in other words, the specific dynamic action should disappear (see Fig. 1).

The results shown in Table VIII are not in accordance with this theory. Although 21°C. is considered an extremely low temperature for baby chicks, the specific dynamic action of the food at this temperature is higher than at 32°C. and 38°C. not only in absolute terms but also in per cent of the available energy of the food consumed.

This result may be explained partly by the possibility that the chicks can decrease their heat requirement by huddling together. It has been observed in the trial at 27°C. but particularly at 21°C. that when the chicks are not eating, they gather in a corner of the cage, forming a pyramid. This huddling of the chicks at low temperature decreases their heat loss 15 per cent (Kleiber and Winchester, 1933). It is to be regarded as a third kind of temperature regulation which we have termed social temperature regulation. It tends to make the basal metabolism at low temperature lower than it would be without this huddling and consequently increases the gap between basal metabolism and metabolism at full feed.

(h) Efficiency of Energy Transformation at Various Temperatures

By efficiency of food utilization may be understood the ratio of an increase in net energy to the increase in food necessary to produce this net energy

$$\eta_p = \frac{\Delta A}{\Delta U}$$

η_p may be classified as partial efficiency if ΔA is a difference in net energy and ΔU the corresponding difference in food energy. Food energy may be taken as the energy of the food intake, the digested energy, or the available energy.

TABLE IX
Partial Efficiency for Growth in Baby Chicks at Various Temperatures

Air temperature, °C.....	21	27	32	38	40	40
Net energy per 100 Cal. of available food energy.....	57	64	67	72	58	62

On the other hand, efficiency may also mean the ratio of the total net energy to the total food energy.

$$\eta_t = \frac{A}{U}$$

In contradistinction to the partial efficiency, η_t may be called the *total efficiency*. The partial efficiency is always positive. Recent results show that it varies with the plane of nutrition, being somewhat higher at low levels.⁷ It is positive also in undernutrition, as a decrease in the loss of body substance due to an increase in food consumption may be taken as an increase in net energy. The determination of the partial efficiency requires the measurement of the metabolism at two dif-

⁷ In an experiment of Forbes *et al.* (1930) the partial efficiency dropped from 87 to 64 per cent of the metabolizable energy as the plane of nutrition was increased from $\frac{1}{2}$ maintenance to 3 times maintenance. Wiegner and Ghoneim (1930) applied Mitscherlich's law to the partial efficiency of food utilization in animals.

ferent food levels. One level may be at zero. Thus, in the case of the chicks in the experiments discussed here, the basal metabolism and metabolism at full feed are used. The increase in net energy in this sense is the difference between the increase of the available energy and the heat increment. Thus Table IX is calculated from Table VIII.

The partial efficiency is subject to a relatively large experimental error. From Kellner's data (Kellner and Köhler, 1900) it may be calculated that the standard error for the partial efficiency of starch for fattening adult steers is ± 11 per cent of the mean. The deviation between the results of the two chick trials at 40°C. is ± 6.7 per cent of the mean. The increase in efficiency from 57 per cent at an air temper-

TABLE X
Total Efficiency of Energy Utilization in Growing Baby Chicks at Various Temperatures

Air temperature, °C.....	21	27	32	38	40	40
Total efficiency $\left(\frac{\text{Net energy} \times 100}{\text{Available food energy}} \right)$..	16	28	34	33	32	26

ature of 21°C. to 72 per cent at an air temperature of 38°C., a difference of 23 per cent of the mean, appears thus to be barely significant.

The total efficiency is related to the partial efficiency according to the following equation:

$$\eta_t = \frac{A}{U} = \frac{\eta_p(U - E)}{U} = \eta_p \left(1 - \frac{E}{U} \right)$$

where

- η_t = total efficiency
- η_p = partial efficiency
- U = energy of food intake
- E = energy of food for maintenance.

At a given partial efficiency the total efficiency increases with increasing plane of nutrition. It becomes zero when the total food energy is equal to the energy necessary for maintenance.

Since the total efficiency in our trials is determined independently

of the basal metabolism, the influence of the social temperature regulation on the basal heat production does not affect the results of the total efficiency. Therefore, these results calculated from Table V are less questionable than those on the partial efficiency.

The total efficiency reaches its maximum at 32°C. The environmental temperature had a more pronounced influence on the total efficiency than on the partial efficiency. 16 per cent total efficiency at 21°C. is only 47/100 of the maximum total efficiency at 32°C., whereas 57 per cent partial efficiency at 21°C. is 79/100 of the maximum partial efficiency at 38°C.

DEDUCTION

From general considerations it has been concluded that an optimal environmental temperature for the conversion of food energy to the energy of body substance should exist not only for cold blooded but also for warm blooded animals. At extremely low environmental temperature all the energy which an animal is able to absorb is used as heat for maintaining the body temperature at a constant level; at extremely high outside temperature theoretically the animal's appetite is decreased to such an extent that the energy intake does not exceed the maintenance requirement.

In our experiments with baby chicks we did not reach either of these extremes. We found that within the range of temperatures covered in our investigation the total food intake was a linear function of the environmental temperature and not a curve as suggested in Fig. 1. A curve of the expected type has, however, been obtained for the intake of metabolizable energy due to the limitation of the absorbing power of the intestinal tract. At high environmental temperature the appetite was decreased. In accordance with the preliminary hypothesis the heat production of the animals tended to approach the intake of metabolizable energy at high as well as at low environmental temperature. The prediction of an optimal environmental temperature for the efficiency of energy utilization is thus supported by the results of our trials.

SUMMARY

1. An optimum of environmental temperature is to be expected for the utilization of food energy in warm blooded animals if their food intake is determined by their appetite.

2. Baby chicks were kept in groups of five chicks in a climatic cabinet at environmental temperatures of 21°, 27°, 32°, 38°, and 40°C. during the period of 6 to 15 days of age. The intake of qualitatively complete food was determined by their appetite. Food intake, excretion, and respiratory exchange were measured. Control chicks from the same hatch as the experimental groups were raised in a brooder and were given the same food as the experimental chicks. The basal metabolism of each experimental group was determined from 24 to 36 hours without food at the age of 16 days.

3. The daily rate of growth increased with decreasing environmental temperature from 2.74 gm. at 40°C. to 4.88 gm. at 21°C. This was 4.2 to 6.5 per cent of their body weight.

4. The amount of food consumed increased in proportion to the decrease in temperature.

5. The availability of the food, used for birds instead of the digestibility and defined as $\frac{\text{Food-excreta}}{\text{Food}}$ showed an optimum at 38°C.

6. The CO₂ production increased from 2.95 liters CO₂ per day per chick at 40°C. to 6.25 liters at 21°C. Per unit of the 3/4 power of the body weight, 23.0 liters CO₂ per kilo^{3/4} was produced at 40°C. and 43.4 liters per kilo^{3/4} at 21°C. The CO₂ production per unit of 3/4 power of the weight increased at an average rate of approximately 1 per cent per day increase in age. The R.Q. was, on the average, 1.04 during the day and 0.92 during the night.

7. The net energy is calculated on the basis of C and N balances. A maximum of 11.8 Cal. net energy per chick per day was found at 32°C. At 21°C. only 6.9 Cal. net per day per chick was produced and at 40°C. an average of 6.7 Cal.

8. The composition of the gained body substance changed according to the environmental temperature. The protein stored per gram increase in body weight varied from 0.217 to 0.266 gm. protein and seemed unrelated to the temperature. The amount of fat per gram gain in weight dropped from a maximum of 0.153 gm. at 32°C. to 0.012 gm. at 21°C. and an average of 0.107 gm. at 40°C. The energy content per gram of gain in weight had its maximum of 2.95 Cal. per gm. at 38°C. and its minimum of 1.41 Cal. per gm. at 21°C. at which temperature the largest amount of water (0.763 gm. per gm. increase in body weight) was stored.

9. The basal metabolism increased from an average of 60 Cal. per kilo^{3/4} at an environmental temperature of 40°C. to 128 Cal. per kilo^{3/4} at 21°C. No indication of a critical temperature was found.

10. The partial efficiency, *i.e.* the increase in net energy per unit of the corresponding increase in food energy, seemed dependent on the environmental temperature, reaching a maximum of 72 per cent of the available energy at 38°C. and decreasing to 57 per cent at 21°C. and to an average of 60 per cent at 40°C.

11. The total efficiency, *i.e.* the total net energy produced per unit of food energy taken in, was maximum (34 per cent of the available energy) at 32°C., dropped to 16 per cent at 21°C., and to an average of 29 per cent at 40°C.

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