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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

V. The Effect of Temperature on the Percentage-Rate of Growth of the Chick Embryo

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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

V. The Effect of Temperature on the Percentage-Rate of Growth of the Chick Embryo*

EARL W. HENDERSON AND SAMUEL BRODY

ABSTRACT.—Eggs were incubated at four different temperatures (94°, 95°, 99°, and 105°F), and the chick embryos weighed daily, beginning with the fourth day of incubation. The results of this work indicate that temperature exerts a profound influence on the percentage-rate of growth and that this influence varies with the stage of incubation. These facts are expressed in quantitative forms by means of charts and equations, and their biological significance is discussed.

In the preceding bulletin (Research Bulletin 98) of this series, it was shown that the percentage-rate of growth of the chick embryo tends to remain constant during certain intervals; and that there are well defined breaks between these intervals of constant growth rate. However, the percentage-rates of growth and the ages at which the breaks in the curves occur were found to be different in growth curves constructed from data obtained by different investigators, even if the same breeds of birds were used. Since in the earlier stages of growth the heat-regulating mechanism is not well developed, it was suggested that the differences in the results may have been due to differences in the incubation temperatures employed. The principal purpose of the present bulletin is to substantiate this suggestion by means of growth curves of chick embryos incubated at varying temperatures. A second purpose is to present data for temperature coefficients of growth in the early life of warm blooded animals.

The literature relating to the effect of temperature on life processes has been recently reviewed by Kanitz[1]. It remains for us only to point out several references and facts which have a direct bearing on the present problem.

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The physiological zero for incubation, that is the temperature below which development will not begin in the hen's egg, was found by Edwards[2] to be between 20° and 21°C (68°-70°F).

The effect of temperature (between 30° and 40°C) on the rate of heart beat in the chick has been investigated by Cesana[3] who found the value of Q_{10} to vary from 1.32 to 2.63.

On the basis of observations relating to the effect of temperature on carbon dioxide excretion in the chick embryo, Pembrey and Gordon[4] concluded that during the first 20 days of incubation the chick behaves like a cold blooded animal.

There is no general agreement concerning the optimum incubation temperature for the chick embryo. Phillips and Brooks[6] recommend 101°F (38.3C) for the type of incubation employed in this work. Manufacturers of incubators of the size employed in the present work, and of incubators of the sectional type in general, recommend 103°F (39.4C). A much lower temperature, 99°F(37.2°C), is usually employed for incubators of the cabinet type.

In interpreting the growth curves, it will be useful to keep in mind the fact that the body temperature of the adult fowl ranges from 40.0° to 42.5°C. (Av. 41.2°C or 106°F).

METHODS AND RESULTS

The eggs were incubated in a 150-egg size, hot air, Prairie State incubator. This incubator was fitted with a self recording thermometer (graduated in Fahrenheit units). The center of the thermometer bulb was three centimeters above the bottom of the egg tray. The top of the bulb was level with the top of the eggs. The normal range in variation of temperature was about .2°F, but several times this range was exceeded for several hours at a time. In the commercial incubation of eggs, it is customary to increase the temperature with the advance of the incubation period. In these observations, however, the temperature was kept constant throughout the whole period.

The eggs were from Single Comb White Leghorn hens, one year old or over. Previous to incubation, the eggs were stored at a temperature varying from 40° to 70°F (that is below the physiological zero) for from 7 to 9 days. The ages of the embryos are expressed in terms of incubation age.

The embryos were weighed after removing the amniotic membranes and draining the amniotic fluid.

In the early stages ten embryos were taken for a weighing. With the increase in the weight of the embryos, and consequent decrease in the percentage error of the determinations, the number of embryos taken for a weighing was gradually reduced.

At 90°F (32.22°C) 148 eggs were set. All the embryos were found dead the tenth day.

At 94°F (34.44°C) 148 eggs were set. Twelve embryos were used in making the weighings on the 10th and 12th days. The remaining embryos were found dead on the 14th day.

At 95°F (35°C) 148 eggs were set. Of these, 10 were infertile, 41 embryos died during the course of incubation, and 97 were used for weighing. The high mortality at this temperature made it necessary to skip several weighings in order to insure enough survivors for the later stages.

At 99°F (37.22°C) 148 eggs were set. Eleven eggs were found to be infertile; 24 embryos died during the course of incubation; 113 were weighed. Hatching occurred on the 22nd instead of the usual 21st day.

At 105°F (40.55°C) 140 eggs were set. Nineteen were found to be infertile; 27 embryos died during the course of incubation and 94 embryos were weighed.

The numerical data for weights are presented in Table I.

ANALYSIS OF DATA

Employing the method of analysis explained in the fourth bulletin of this series (Research Bulletin 98), the data were plotted with the

TABLE 1.—THE EFFECT OF TEMPERATURE ON THE GROWTH OF THE CHICK

Incubation age	Wet Weight in Grams 94°F (=344°C)	95°F (=35.0°C)	99°F (=37.3°C)	105°F (=40.5°C)
Days				
4				.225
5			.059	.434
6			.189	.909
7			.377	1.376
8		.311	.639	2.032
9		.583	1.234	3.046
10	0.475	.939	1.591	4.113
11		1.323	2.133	6.259
12	1.252	1.730	3.081	8.457
13		2.226	4.292	10.426
14			6.162	13.485
15		3.525	8.758	15.314
16			10.989	18.505
17		5.510	12.685	20.427
18			15.895	
19		8.322	17.529	
20			21.708	
21		11.49	27.133	
22			37.7	

results shown in Fig. 1. The data of Lamson and Edmond[5] were included for the purpose of comparison.

Fig. 1 shows that temperature exerts a profound influence on the numerical values of k (that is on the relative-rates of growth), and also on the position of the breaks in the curves. Fig. 1 leaves no doubt that,

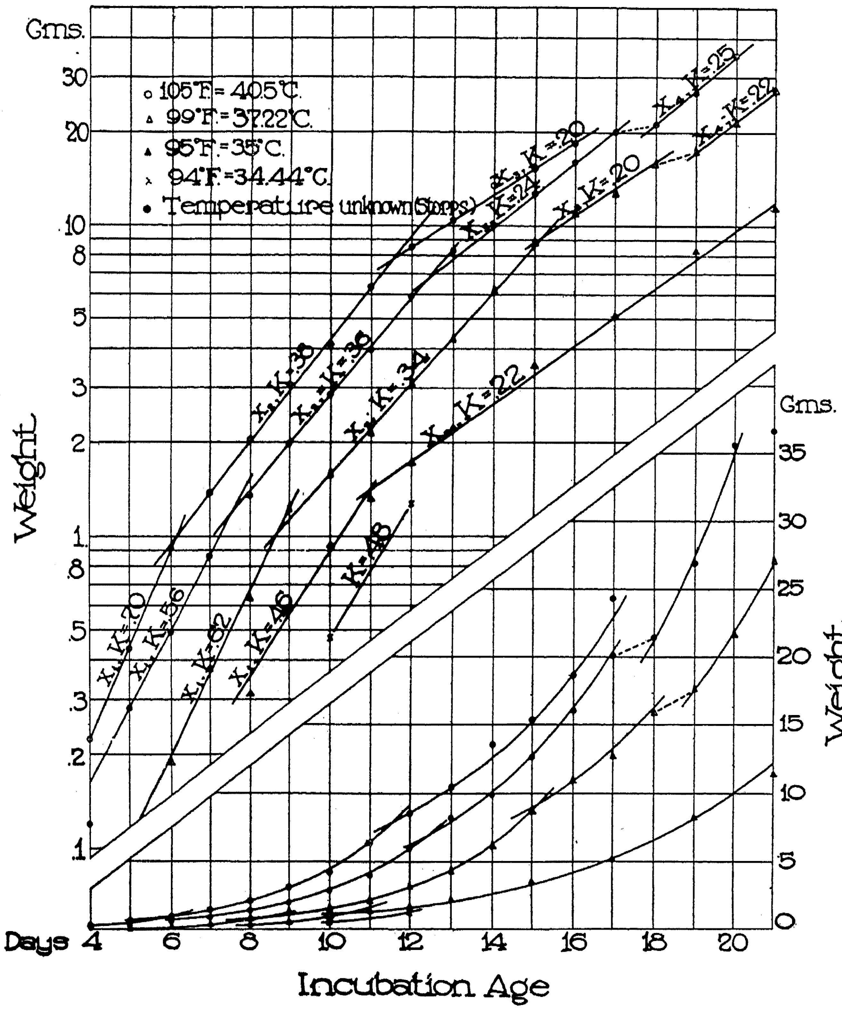

Fig. 1.—Growth of the chick embryo in wet weight at three temperatures. The observed values are indicated by circles, the smooth curves were computed from the formula $W = W_0e^{kt}$. The numerical values of k refer to the relative rates of growth, k, of the above equation. Thus 100 k is the percentage rate of growth referred to the day as the unit of time.

in the earlier stages of growth, the variations in the numerical values of k, and in the positions of the breaks in the curves as found in the preceding bulletin, have been caused by differences in the incubation temperatures.

While the primary purpose of presenting these data at this time is to substantiate the idea that growth within certain limits tends to take place at a constant percentage-rate, it is worth while to discuss the data also with reference to the significance and nature of the temperature effect. We are not aware of investigations concerned with the effect of temperature on the rate of growth of the young of warm blooded animals. The results of this investigation should, therefore, be useful in throwing light on several phenomena as: (1) the time relations of development of the heat-regulating mechanism in the young of warm blooded animals; (2) the functional relation between the development of the heat-regulating mechanism and the ability of the animal to withstand low temperature; (3) the temperature limits between which growth occurs; (4) the temperature for optimum growth; (5) the relation between the optimum temperature for growth and the body temperature of the mature animal; (6) the nature of the mechanism limiting growth, whether it is, for example, physical or chemical (7) the effect of temperature on the numerical values of rates of growth at different stages of growth. These ideas are discussed in the following paragraphs.

To obtain a numerical value relating the rate of growth to temperature, we have plotted in Fig. 2 the relative-rates of growth, k, against the corresponding temperatures, t. Since the growth curve is made up of several distinct phases, it is, of course, necessary to plot the curve for each growth phase separately. The growth curves in Fig. 2 are marked by X_1, X_2, and X_3 corresponding respectively to the segments X_1, X_2, and X in Fig. 1.

In Fig. 2, curve X_1, representing the effect of temperature on the earliest phase of growth, is the steepest curve of the three; that is, temperature has a greater effect on the earliest segment of the curve than on the latter two. Curve X_2 is less steep than its predecessor X_1, and curve X_3 is horizontal. The fact that curve X_3 is horizontal probably means that the heat regulating mechanism in the chick is sufficiently developed at this stage to enable it to keep its body temperature constant within the limits of 37.2° and 40.6°C. The fact that the chicks did not survive this stage at 35°C., probably means that the chick could not compensate for the lowered temperature at this temperature and that it is more sensitive to a lowering of body temperature at this stage of growth than in the preceding stages. In other words, the animal is not strictly cold blooded at this stage. By the same line of reasoning it is

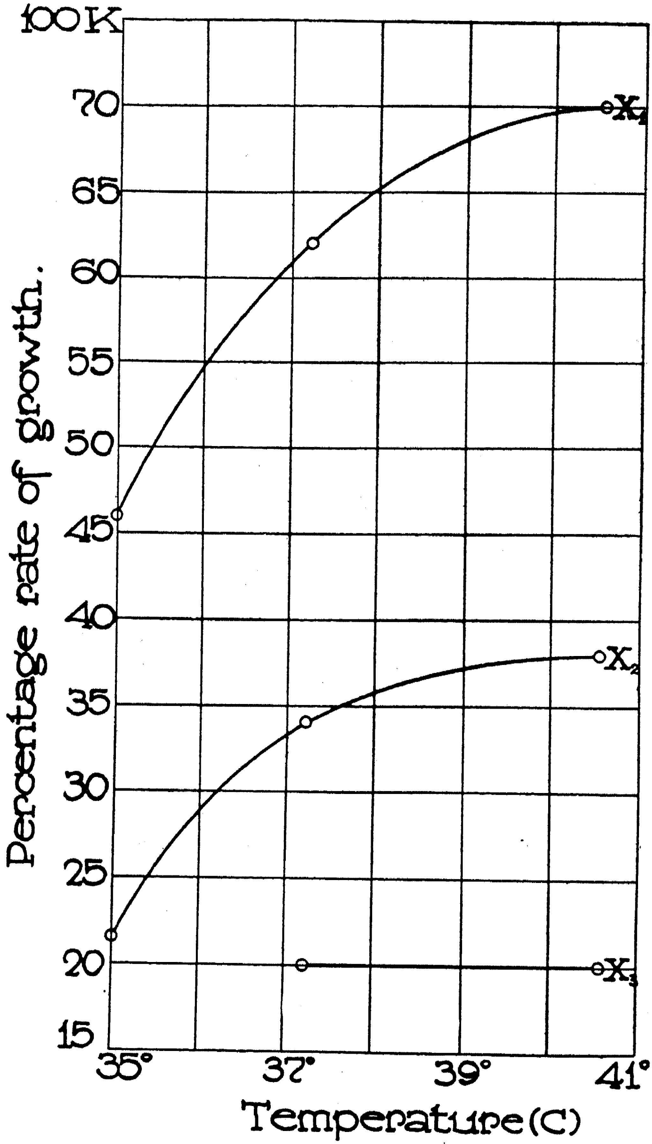

Fig. 2.—The relation between temperature and the relative-rate of growth, k, for phases X_1, X_2, and X_3. (*cf.* Fig. 1).

inferred that the chick is less capable of controlling its temperature during phase X_2 than during phase X_3; and during phase X_1 less than during phase X_2, thus resulting in higher temperature coefficients, that is steeper curves, for the earlier phases of growth as shown in Fig. 2.

The shapes of the curves in Fig. 2 indicate that the rate of growth does not increase with temperature in a *simple* exponential, logarithmic, or linear relationship. Since the formulae employed for obtaining temperature coefficients are based on some one of these assumed relationships, none of the formulae recorded in the literature on temperature coefficients, can properly be employed for evaluating temperature coefficients for the curves in Fig. 2.

It does not appear advisable to devise a new formula on the basis of three data points given in Fig. 2, so we have simply computed temperature coefficients as defined by formulae given in the literature, or as derived from such formulae, leaving the more rigorous evaluation of the temperature coefficients to a later time when more adequate data may be available.

The temperature coefficients, expressed in terms of u and Q_{10}, are given in Table II. They were computed by the use of the following four formulae:

$$\text{I:}\quad Q_{10} = 1 + \frac{k_2 - k_1}{\frac{1}{2}(k_2 + k_1)} \times \frac{10}{(t_2 - t_1)}$$

Formula I, of our own devising, represents the rate of growth to increase linearly with temperature. The term k_2 is the relative rate of growth at temperature t_2; and k_1 at temperature t_1.

$$\text{II:}\quad Q_{10} = 1 + (\ln k_2 - \ln k_1) \times \frac{10}{(t_2 - t_1)}$$

Formula II, represents the rate of growth to increase exponentially with temperature.

$$\text{III:}\quad Q_{10} = \frac{k_2}{k_1}^{\frac{10}{t_2 - t_1}}$$

$$\text{IV:}\quad u = \frac{2T_1T_2(\ln k_2 - \ln k_1)}{T_2 - T_1}$$

Formula IV, is the well known equation of Arrhenius.

For the earlier stages of growth, and for the lower temperature regions, the values of Q_{10} fall within the limits of the values of Q_{10} for ordinary chemical reactions (*cf.* Kanitz[1]). Similarly the values of *u* fall within the limits of the values of *u* for chemical reactions (*cf.* Arrhenius[1] pp. 54-55). These facts may be taken as evidence in favor of the hypothesis that a chemical mechanism limits the rate of growth in the early life of the chick.

TABLE 2.—TEMPERATURE COEFFICIENTS OF GROWTH OF THE CHICK EMBRYO

Growth phase (see Figs. 1 and 2)	Temperature °C	Instantaneous percentage rate of growth per day, 100 *k*	Temperature coefficient			
			Q_{10}			*u*
			Formula I	Formula II	Formula III	Formula IV
X_1	35.0	46				
			2.33	2.35	3.83	25,700
	37.22	62				
			1.36	1.36	1.44	7,100
	40.55	70				
X_2	35.0	22.6				
			3.46	3.04	7.72	39,050
	37.22	34				
			1.33	1.36	1.40	6,500
	40.55	38				
X_3	37.22	20				
			0	0	0	0
	40.55	20				

SUMMARY AND CONCLUSIONS

Data on growth in total weight of the chick embryo indicate that the chick passes through several distinct growth stages. The percentage-rate of growth is constant during each of the stages. Each stage of growth passes rather abruptly into a successive stage of a lower percentage-rate of growth.

The rates of growth, as well as the lengths of each growth stage, are variously affected by temperature, depending on the age of the chick and on the temperature employed. Before the age of about 13 days, and between the temperatures of 35° and 37°C., an increase in the temperature by 1°C results in an *average* increase in the rate of growth of between 13 and 20 per cent (that is Q_{10} = 2.3 to 3.0 assuming that between these limits the rate of growth increases exponentially or linearly with temperature).

After the stage of growth corresponding to about 13 days at normal incubation temperature, changes in temperature within the limits of 37 and 41° C. did not influence the rate of growth. The temperature coefficient (Q_{10}) in the early stages of growth and at the lower temperature regions exceeds the value of 2.0. (That is, an increase in the incubation temperature by 10°C more than doubles the percentage-rate of growth.) The bearing of these facts on the development of the temperature regulating mechanism and on the nature of the growth process is discussed in the text.

REFERENCES

1. Kanitz, A., *Temperaturabhangigkeit der Lebensvorgange* . .R G T—Regel (Reprint from Oppenheimer, C., Handbuch der Biochemie 2. Aufl. Bd. II, (1923); Arrhenius, S., Quantitative Laws in Biological Chemistry, London, 1915; Mellor, J. W., Chemical Statics and Dynamics, London, New York, Bombay and Calcutta, 1909.
2. Edwards, C. L., Am. J. Physiol, 1901-2, VI, 351.
3. Cesana, G., Arch. di. Fis. 1921, X, 193, cited by Kanitz[2].
4. Pembrey, M. S., Gordon, M. H., and Warren, R., J. Physiol., 1894-5, XVII, 331.
5. Lamson, G. H., and Edmond, H. D., Storrs Agric. Exp. Station, Bull. 76, 1914.
6. Phillips, A. G., and Brooks, F. D., Purdue Univ. Agric. Exp. Sta. Bull. 275, 1923.