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GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

IV. Growth Rates During the Self-Accelerating Phase of Growth

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FOREWORD

Investigations on the subject, "Growth and Development with Special Reference to Domestic Animals," have been in progress for some time at the Missouri Agricultural Experiment Station. Reports on special phases of this general subject will be published as they are completed. The present paper, though numbered fourth in the series, is the third to be published.

ACKNOWLEDGMENT

A portion of the expenses involved in this investigation was paid from a grant from the Committee on Food and Nutrition of the National Research Council. Grateful acknowledgment is made for this cooperation, which was received through the recommendation of Dr. Lafayette B. Mendel, chairman, and Dr. E. B. Forbes, chairman of the Subcommittee on Animal Nutrition.

GROWTH AND DEVELOPMENT

With Special Reference to Domestic Animals

IV. Growth Rates During the Self-Accelerating Phase of Growth*

SAMUEL BRODY

ABSTRACT.—The period of growth may be divided into two phases: (1) A *self-accelerating phase* during which the time-rate of growth increases with the increase of the size of the organism; and (2) A *self-inhibiting phase* during which the time-rate of growth decreases while the size of the organism increases. The present bulletin presents analyses of growth curves of the *self-accelerating phase* of growth. These analyses brought to light the following facts: (1) in warm-blooded animals this part of the curve is made up of several (4 or 5) segments apparently representing distinct stages of growth; (2) the percentage-rate of growth during each of these stages is constant; (3) each stage of constant growth rate passes into a succeeding stage of a lower, but constant, percentage-rate; (4) the passage from one stage to the other is abrupt, the abruptness being of the order found in metamorphosis in cold-blooded animals.

INTRODUCTION

1. **Summary of the Preceding Bulletin.**—In the preceding bulletin (Research Bulletin 97) of this series it was explained that the growth curve is sigmoid in form, and that it may be divided into two major segments: (1) a segment of increasing time-rate of growth embracing the period between conception and puberty; and (2) a segment of decreasing time-rate of growth comprising the remaining portion of the growth curve.

It was explained that the increase in the time-rate of growth is due to a mechanism inherent in the reproducing units of the organism which causes them to reproduce at (statistically) equal intervals of time (in the absence of disturbing factors), and thus to grow at a constant percentage-rate. A constant *percentage-rate* of growth, of course, implies an increasing *time-rate* of growth. Growth preceding the inflection is thus a self-accelerating process; the greater the number of reproducing units, the greater the absolute number of progeny produced per unit of time; and the larger the body, the faster it grows.

In the preceding bulletin the general properties of the self-accelerating phase of growth were discussed. The conclusions arrived at were illustrated by an analysis from this point of view, of data on growth of

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*The writer owes a debt of gratitude to Dean F. B. Mumford and to Professor A. C. Ragsdale for their encouragement and continuous interest in this work.

the albino rat. The purpose of this bulletin is (1) to present additional evidence substantiating the conclusions in the preceding paper, and (2) to present numerical values of true percentage-rates of growth during the self-accelerating phase of growth.

The general conclusion arrived at in the preceding bulletin relating to the self-accelerating phase of growth of higher animals, is that it consists of several periods, or epochs, and that during each of these epochs, the percentage-rate of growth is, within the limits of experimental error, constant.

It was explained that the best way to determine the constancy in percentage-rate of growth is to plot the weights against age on arithlog paper. Whenever the percentage-rate of growth is constant, the data points will be distributed about a straight line.

2. The Significance of the Earlier Stages of Growth for the Evaluation of Growth-Rates.—There are several reasons for considering the earlier stages of growth as very significant from the point of view of growth-rates. In the first place, the percentage-rate of growth is then most rapid, and a unit of time is, so to speak, a much longer period in an earlier than in a later stage of growth; a unit of time in the earlier stages represents the birth of a greater number of generations of cells, and consequently a longer ontogenetic history than a unit of time in later stages represents.

A second reason for the relatively greater importance of a knowledge of the growth-rates during the earlier stages of growth, is that the maximum growth-potential, or growth-intensity, inherent in the reproducing units of different species can be determined only during the earlier stages; for with advancing age, growth-retarding forces develop in the organism which mask the original genetic growth potentials of the species. A knowledge of the maximum growth-intensities, or the frequencies of cell division, in different species would evidently be of much interest to the physiologist—comparable, for example, to the interest of the physical chemist in the relative electromotive forces of different elements.

A third reason for the relatively greater significance of the shape of the growth curve in the earlier stages of life is that, as pointed out, the segment of the growth curve preceding the major inflection is made up of several stages, or epochs, each having a characteristic percentage-rate of growth. The succession of these stages is relatively abrupt. The suggestion was made in the preceding bulletin that the abruptness of successions may be brought about by a succession of threshold mechanisms (due for example to glands of internal secretion). A careful study of the percentage-rate curves should, therefore, form a guide to the investigation of the threshold mechanisms, if there are such.

The relatively rapid succession of growth-stages in early life makes it necessary to use great caution in their investigation. For there is always the danger of mistaking a decline in the percentage-rate of growth due to a transition from one stage, into another stage of a lower potential of growth, for a decline during a given stage. This is the principal reason against the use of Minot's method of computing percentage-rates of growth. It is also for this reason that it is advisable to make the intervals between measurements as brief as possible.

From an analytic point of view, too, it is the earliest stages having the greatest percentage-rates of growth which offer the best opportunity for the determination of the laws of growth. It is only when the rates of change are relatively high that there are significant differences between, for example, curves of linear and of exponential change. When the percentage-rate of growth is less than 10 per cent for the unit of time under consideration, it is not possible to differentiate between the two types of changes, and it is not, therefore, possible to determine the law of growth.

On account of the considerations named above, it seems desirable to make a careful study of the available data on early growth, even if the data are far from being adequate as a basis for drawing final conclusions concerning the nature of growth rates.

II. GROWTH OF THE ALBINO RAT

The available data on early growth of the albino rat have already been discussed and presented in graphic form in Figs. 5 and 6 of the preceding bulletin of this series.

Figure 5 of the preceding bulletin indicates that during the interval of 13 and 21 days after conception, the percentage-rate of growth is constant. Growth takes place at the approximate rate of 53 per cent per day. If the percentage-rate of growth is known, it is possible, as explained in the preceding bulletin, to determine the time required for the body weight to double itself. The time required for the body weight to double itself, is the ratio of the natural logarithm of 2, namely, 0.69315... to the relative-rate of growth, *k*. The value of *k* between 14 and 21 days after conception is .53; therefore the weight of the body is doubled at intervals of

$$\frac{.69}{.53} = 1.3 \text{ days.}$$

If growth in weight is directly proportional to the increase in the number of cells in the body, then a new generation of cells is produced, on the average, but once in 1.3 days; or the cell division frequency is $\frac{1}{1.3} = .77$ per day. This is a much lower value than the reader familiar with the literature on growth anticipated. There is a possibility that the actual frequency of cell division is higher than the frequency as thus computed for the reason that there is a decrease in the concentration of water in the body with advancing age; but against this decrease in the percentage of water, one must consider the increase in relatively inert substances, such as skeletal structures, with increasing age.

At birth, Fig. 5 of the preceding bulletin indicates there is a sudden drop in the percentage-rate of growth. Using the terminology of Davenport in a figurative sense, we may say that the animal undergoes a metamorphosis at this time. True metamorphosis, of course, signifies a relatively abrupt change in form as well as in growth rate. The changes in form, if any, at this time in the animals under consideration, will be discussed in a future bulletin of this series.

At birth, the percentage-rate of growth was seen to drop from 53 to about 12 per cent per day; that is, the "quantum" for cell-division increased from 1.3 to at least 5.8 days, or the frequency of cell division dropped from $\frac{1}{1.3} = .77$ to $\frac{1}{5.8} = .18$ per day.

At 10 days after birth there appears to be another abrupt drop, this time to a percentage-rate of 4.5; and a final drop before the major inflection at one month after birth (52 days after conception), to about 3 per cent per day (when it requires, on an average, 23 days for the body to double its weight).

The statements relating to the changes in the rate of growth following 10 days after birth are made tentatively for the reason, explained before, that when the percentage-rate of growth falls below a certain value, it becomes difficult to differentiate between the nature of the growth-rate; for example, whether it is exponential or linear.

The white mouse, which is related to the white rat, also exhibits a growth curve which is similar to that of the rat. The data on post-natal growth of the white mouse by Robertson and Delprat, and by Gates, when plotted on arithlog paper indicates the presence of a break at 7 days (Gates' data) or between 4 and 7 days (data of Robertson and Delprat). Up to this break growth proceeds at 14 per cent per day (the body weight is doubled once in 5 days). Between this break and puberty (which occurs at about 35 days), growth takes place at from 3.5 to 4.5 per cent per day (the body weight is doubled in 14 days).

III. GROWTH OF THE GUINEA PIG

Figure 1 shows the course of prenatal growth of the guinea pig plotted on arithlog and on arithmetic paper.

For this purpose data by three investigators working independently were utilized. Dr. Heman L. Ibsen's data have not yet been published. (The writer takes this opportunity to thank Dr. Ibsen for permission to utilize his data for the present purpose). Draper's data were published in 1920. Hensen's data were published in 1868. It is remarkable that the three sets of data should agree so well.

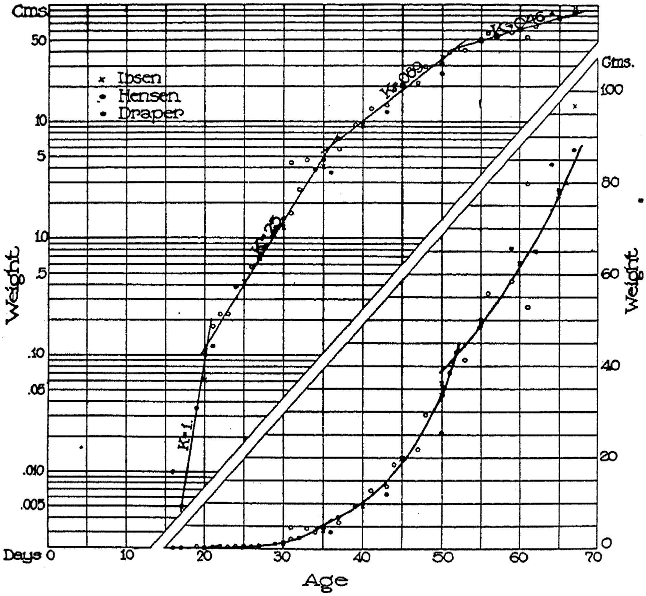

Fig. 1.—Prenatal growth of the guinea pig, plotted from three sources as indicated on the chart. The curve appears to be made up of four distinct segments representing respectively instantaneous percentage-rates of growth of 100 per cent per day (the body weight is doubled once in .7 day or 17 hours); 25 per cent per day (the body weight is doubled once in 2.8 days); 9 per cent per day (the body weight is doubled once in 7.8 days); and 5 per cent per day (the body weight is doubled once in 15.1 days). NOTE—The lettering of this and the following charts was done by Mr. Raymond Hase.

From 17 to 20 days conceptional age the instantaneous rate of growth appears to be 100 per cent per day. This does not mean that the body weight is doubled once a day; it means that the body weight is doubled in $\frac{.69}{1.0} = .69$ of a day. If weight is a measure of the number of cells, then a new generation of cells is produced once in .69 of a day, about once in 16.6 hours.

This is the highest value for percentage-rate of growth of higher animals so far encountered. It will be recalled that in the rat, the rate of growth is 53 per cent per day from the fourteenth day to birth; that is, the body weight is doubled but once in 1.3 days. Since, however, the smooth curve in the present case is based on only four data points, and since the experimental errors are probably very high at this stage of growth, too much emphasis need not be given to the high value of *k*.

At about 21 days conceptional age, there appears to be a sudden drop in the rate of growth to 25 per cent per day. The body weight is therefore doubled once in 2.8 days.

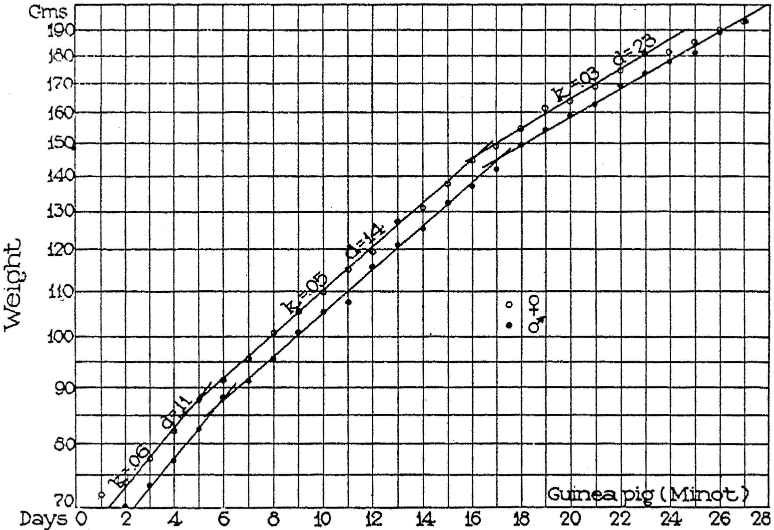

Fig. 2.—Postnatal growth of the guinea pig during the self-accelerating phase of growth (data by Minot). 100 *k* represents the instantaneous percentage-rate of growth per day. *d* represents the time (in days) required for the body weight to double itself.

Another drop occurs at the age of about 37 days, to 8.9 per cent per day (the body weight is doubled once in 7.8 days).

There is probably another drop to a level of 4.6 per cent per day—a level corresponding in the rat to the age interval between 10 and 20 days after birth.

While there is no *a priori* reason for assuming that equal percentage-rates of growth represent equivalent stages in the growth process, it is interesting to note that a guinea pig at birth is approximately as mature as a rat from 2 to 3 weeks after birth. This is inferred from the fact that we have succeeded in raising a considerable number of guinea pigs that were separated from their mothers and placed exclusively on hay and grain ration immediately after birth. These animals have tasted neither colostrum nor milk. Practically all animals weighing over 75 grams at birth survived, and later thrived on this diet (alfalfa hay, and a mixture of 4 parts ground corn, 1 part wheat bran, 1 part linseed oil meal, and 1 per cent salt). In the case of the guinea pig and rat, equal percentage-rates of growth apparently indicate approximately equivalent stages of maturity.

IV. GROWTH OF THE DOMESTIC FOWL

1. Growth in Weight of the Chick Embryo.—Figure 3 represents the wet-weight data on the growth of the chick, collected by Lamson and Edmond at the Storrs Agricultural Experiment Station. There appear to be at least three breaks in the curve between 5 days and hatching.

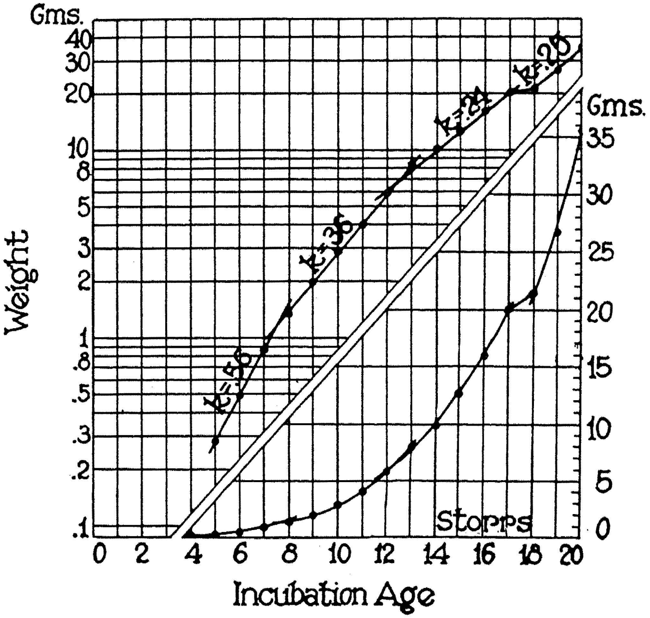

Fig. 3.—Growth in wet weight of the chick embryos, plotted from data by Lamson and Edmond. The curve appears to consist of four segments, each of which represents growth at a constant percentage-rate. The pause in the curve between 17 and 18 days coincides approximately with the second peak in the Mortality curve (Fig. 8). Growth at an instantaneous rate of 56 per cent per per day, indicates that the body weight is doubled in 12 days; at 36 per cent the body weight is doubled once in 1.9 days; at 24 per cent per day, the body weight is doubled once in 29 days.

Between 5 and 7 days, the rate of growth is 56 per cent per day (the body weight is doubled once in 1.2 days). Between 8 and 13 days, the rate of growth is 36 per cent per day (the body weight is doubled once in 1.9 days). During the remaining period preceding hatching, growth appears to take place at about 24 per cent per day (the body weight is doubled once in 2.8 days).

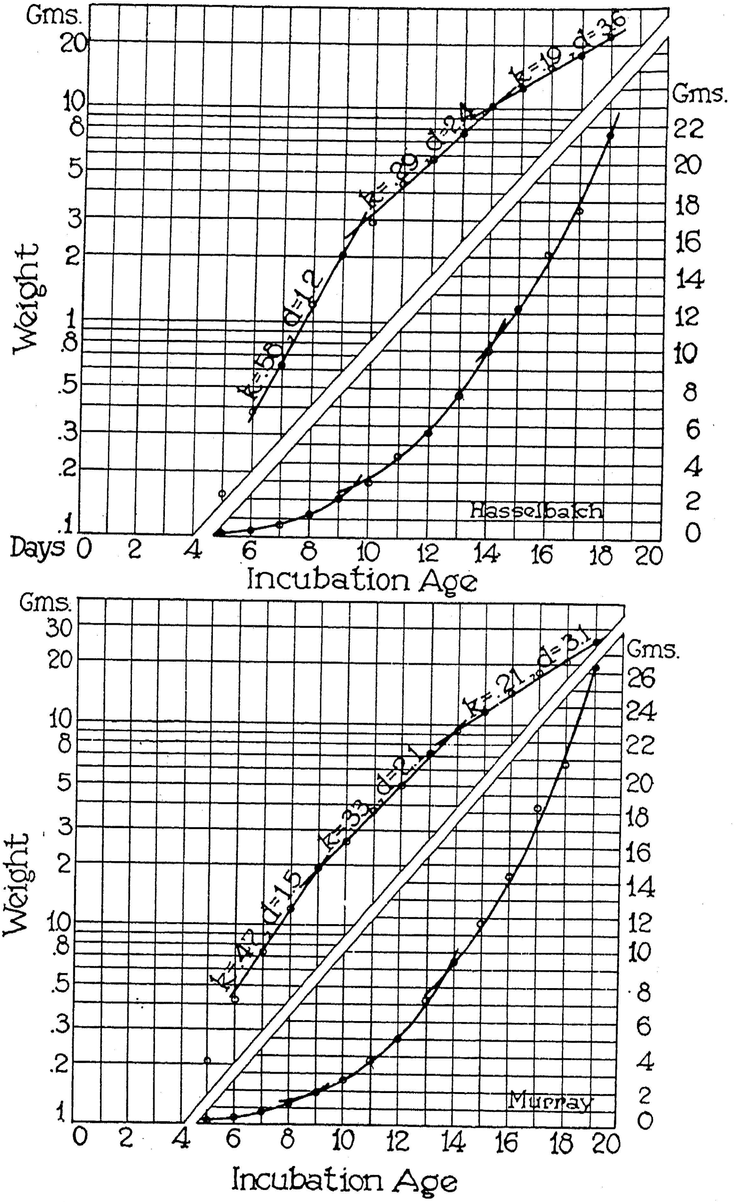

FIG. 4.—Growth in wet-weight of the chick embryo plotted from data by Hasselbalch and by Murray. Compare with Fig 3. The values of 100 *k* represent the instantaneous percentage-rates of growth per day. The values of *d* represent the time in days required for the body to double its weight.

A noteworthy feature of the curve is the pause at the age of approximately 17 days. We shall presently return to a more detailed consideration of this phenomenon.

Figure 4 represents the wet-weight data collected by Hasselbalch and by Murray. In their general features, these curves resemble the preceding curve, but they stop short of reaching the pause. The percentage-rates of growth, and consequently the relative lengths of the corresponding segments, differ from the values found in the preceding curve. These differences are, no doubt, due to differences in the incubation temperatures employed, as will be demonstrated in the following bulletin of this series (Res. Bul. 99).

The curves in Fig. 5 represent the course of growth with respect to several chemical constituents. In the lower chart, the data points represent the products of the percentages of the respective constituents, and the wet weights of embryos as published by Murray. These curves closely resemble the preceding curves for growth in wet weight except that the numerical values of *k* of the corresponding segments are higher for the curves in this chart. In addition to the possible effect of temperature (the data for weight and for the chemical constituents were not obtained on the same individuals, nor under strictly the same temperature conditions) these differences may be due to increase in the percentage of solids with increasing age.

In comparing the curves in Fig. 5, it must be remembered that comparisons must be made for corresponding age, not weight, intervals.

Additional curves for increase in chemical constituents are presented in the upper chart of Fig. 5. Some curves in this chart are noteworthy on account of the high or low values of *k*. Thus the slope of the lime curve is relatively very steep between 12 and 16 days. The value of *k* of the glutathione curve is, on the other hand, relatively low. (Glutathione is a dipeptide of cysteine and glutamic acid recently discovered by Hopkins, and considered to be an important factor in oxidation-reduction reactions). An unexpected feature of the chart is the high value of *k* for urea. The urea in the embryo includes not only the amounts in which it is found as a tissue constituent, but also the accumulation as an end product of protein metabolism. This fact, however, has no relation to the high value of *k* preceding the age of 9 days for the reason that the integral of a simple exponential function is also exponential, having the same value of *k*.

This chart is instructive in bringing out in a striking manner the differential nature of growth. Each system grows at a rate peculiar to itself. However, the differences in the values of *k* are much less than the writer had anticipated.

It is worth while to point out in connection with the discussion of the breaks in the curves at the age of about 10 days, that Willier found

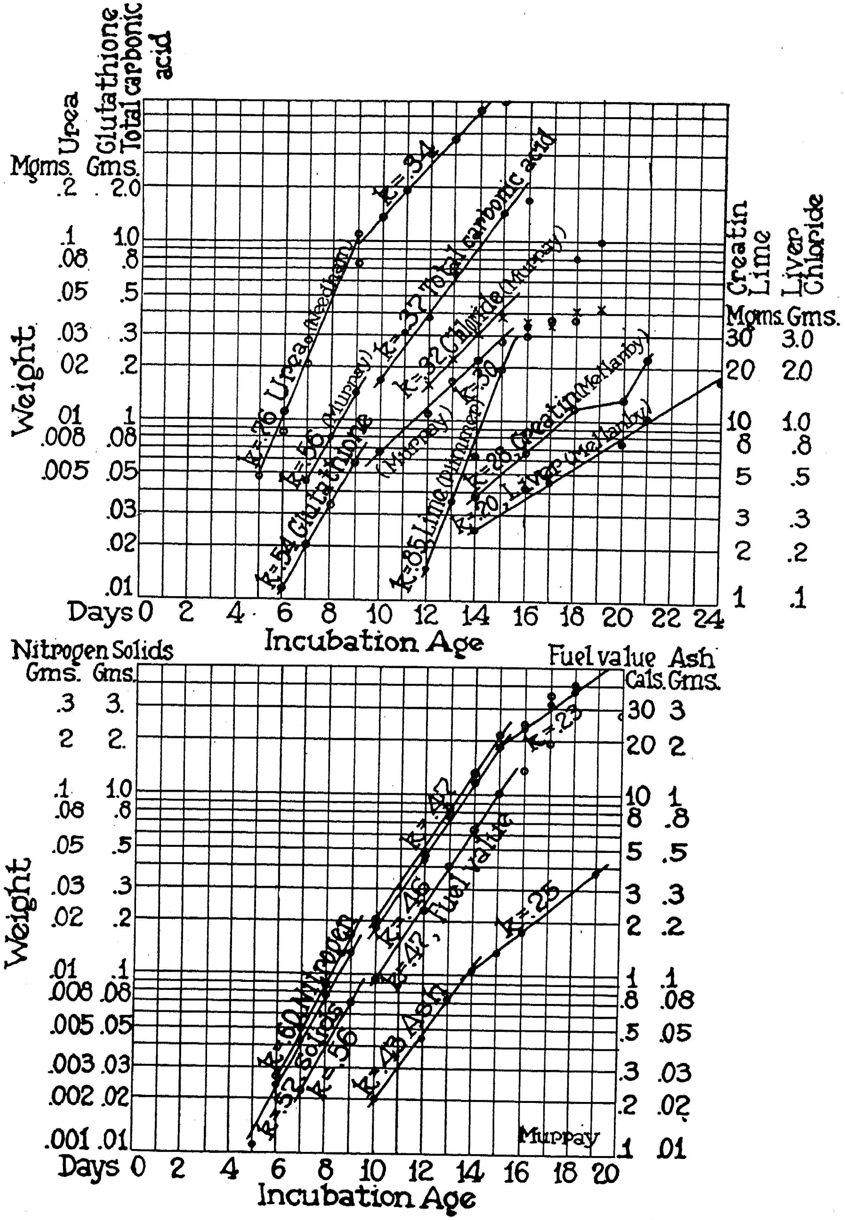

Fig. 5.—The course of increase in chemical constituents in the chick embryo with advancing age The sources of data are indicated on the chart. (Compare with Figs. 3 and 4.)

that "about the eleventh day of incubation a marked increase in vascularity in the thyroid gland takes place and tiny follicles with colloid begin to form". There is a conspicuous break in the curve at 10 days (cf. Fig. 5).

2. Growth in the Chick Embryo Measured by the Course of Carbon Dioxide Excretion.—Data are also available on the course of carbon dioxide excretion in the chick embryo with increasing age. Since there is no definition of growth, from the quantitative point of view,

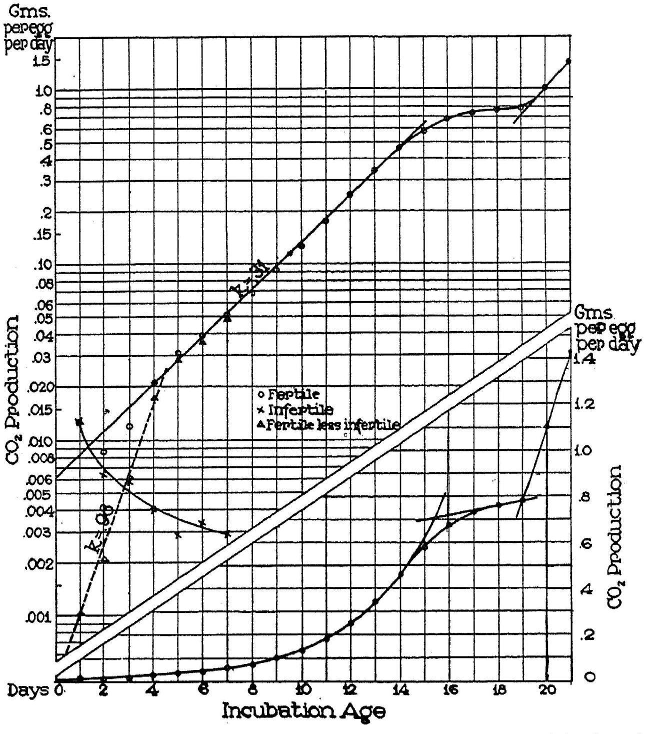

Fig. 6.—The course of carbon dioxide excretion in the chick embryo with advancing age plotted from data by Atwood and Weakley. From 0 to 4 days, the instantaneous percentage-rate of growth appears to be 98 per cent per day (the amount of carbon dioxide excretion is doubled once in .7 day or once in 17 hours); between 4 and 14 days, the rate of increase in carbon dioxide excretion is 31 per cent per day (it is doubled once in 2.2 days). The pause in the curve coincides with the maximum in the mortality curve (cf Fig. 8), and with the change in the mode of respiration (see text).

which is generally accepted, the increase in carbon dioxide excretion with age may be taken as an index of growth-rate. In some respects increase in carbon dioxide excretion is a more satisfactory index of growth than increase in wet or dry weight, since increase in weight may be due to increase in relatively inert, or even non-living matter, while carbon dioxide excretion is generally accepted as an index of metabolizing tissues. The course of carbon dioxide excretion should thus indicate the course of increase of living tissues.

Figure 6 represents the course of carbon dioxide excretion with age in the chick embryo. The curve was plotted from data by Atwood and Weakley. These data are perhaps the best available on the subject. Each egg was incubated in a glass tube by itself, and the carbon dioxide excretion measured daily. The data points represent the average CO_2 output of 63 of such of the eggs as hatched normal chicks.

The circles represent the average carbon dioxide production as reported by Atwood and Weakley. These values are irregular during the first four days. The sudden drop in the carbon dioxide production during the second day is especially conspicuous. The relatively high value for the first day (or what is the same, the relatively low value during the second day) is probably due to the fact that preceding incubation the eggs were kept, as is the custom, in a cool cellar. It is well known that the solubility of gases decreases with increasing temperatures; when, therefore, the eggs were subjected to the relatively high temperature of the incubator, there was in addition to the gas production due to metabolism, also an expulsion of the excess of CO_2 due to its lower solubility at the incubator temperature. This probably accounts for the apparently high CO_2 production during the first and third days of incubation and the low value during the second day.

Data are available for the CO_2 production of an infertile egg, which makes it possible to substantiate the explanation made above. The data for the carbon dioxide excretion of the infertile egg are represented by crosses. The CO_2 output during the first day is seen to be practically the same for the infertile and fertile egg. If the differences between the fertile and infertile eggs (represented by triangles) are plotted, they fall on a fairly straight line of slope, .98. The net rate of increase in the carbon dioxide production mechanism during the first 4 days of incubation is thus seen to be of the order of 100 per cent per day. That is, the carbon dioxide producing mechanism is doubled in magnitude or in intensity once in about .7 day, or in 17 hours.

Figure 7 illustrates the drop in carbon dioxide production during the second day in a more striking manner. In this figure the percentage-increases, 100 $(\ln W_2 - \ln W_1)$, were plotted against age using data from three sources, as indicated on the chart. The greater drop in the curve of Bohr and Hasselbalch is probably due to a lower preincubation temperature employed by these investigators, than by Atwood and Weakley.

Returning to Fig. 6, from 4 to 15 days the data points are distributed in a remarkably uniform manner around a straight line indicating a rate of increase of 31 per cent per day. 31 per cent is approximately the average percentage of the rates of the three segments indicated on the weight curves (Figs. 3 and 4), but the remarkable feature about the carbon dioxide curve is that it does not show the slightest indication of presence of breaks in the curve during this whole, relatively enormous, period between 4 and 15 days. It appears that either the CO_2 producing mechanism develops at a constant percentage-rate independent of the

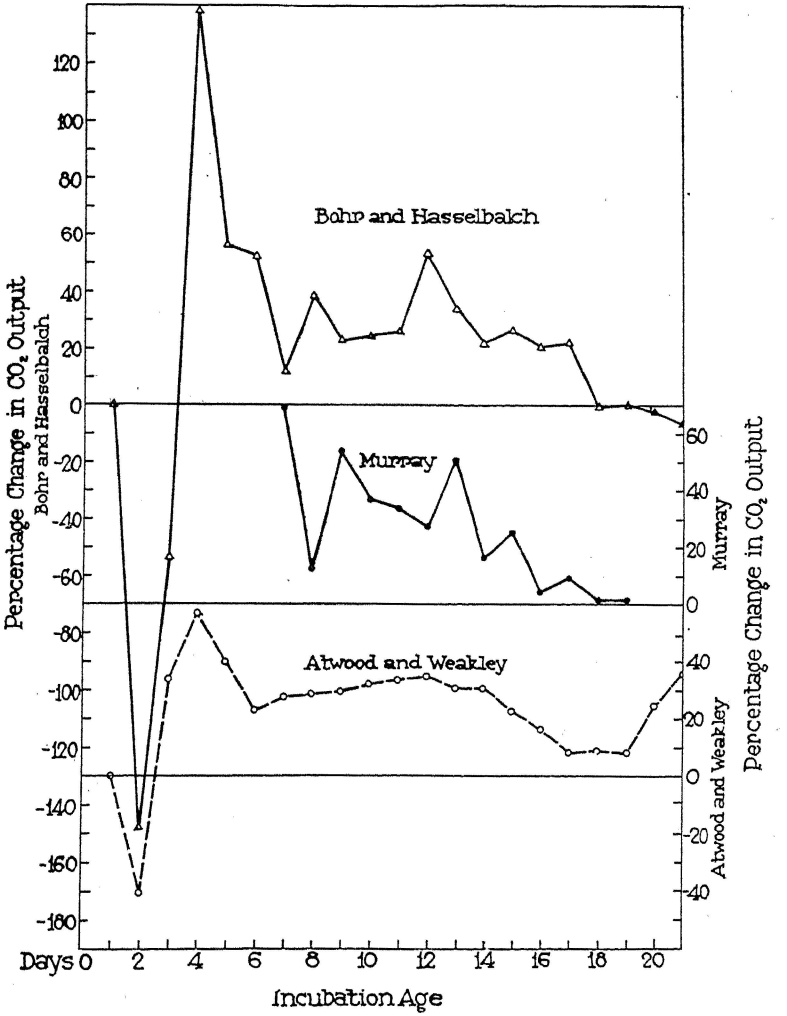

Fig. 7.—Age changes in the percentage-rate increase of carbon dioxide excretion in the chick embryo, plotted from data from three different sources. The numerical values for percentage rates were obtained by subtracting the natural logarithms of the successive values, and multiplying the result by 100 (percentage-rate = 100 (ln W_2 — ln W_1). The cause of the violent changes in percentage-rate during the first 4 days is discussed in the text. Note that the fluctuations in percentage-rate between 4 and 14 days are relatively slight, and that there is no systematic decline in rate during this period. (Compare with Figs. 6 and 9.)

increase in body weight, or that the weight of the body or its constituents can not be taken as an index of the growth of metabolizing tissues. The magnitude or intensity of the CO_2 producing mechanism is doubled once in 2.2 days.

The second remarkable feature of this graph, is the pause between 16 and 19 days. This pause reminds one of the corresponding pause in the weight curve (Fig. 3) at 17 days.

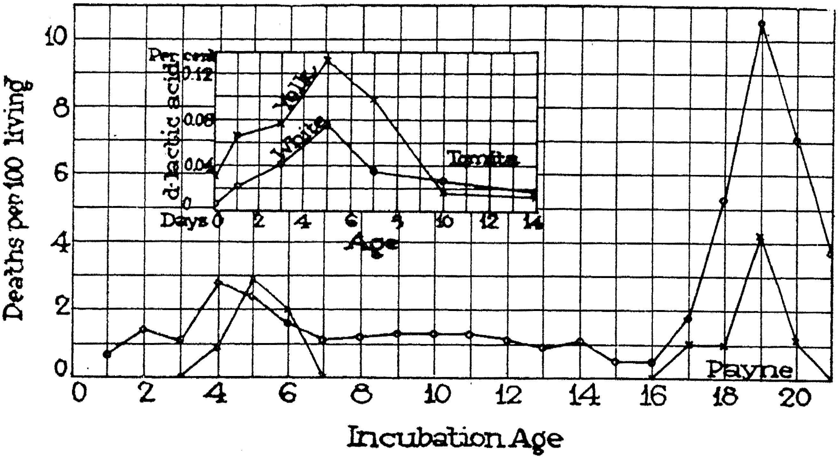

Fig. 8.—Age changes in the percentage mortality with increasing age in the chick embryo. Circles represent mortality data of embryos incubated in an incubator; crosses represent incubation under hens. The first peak in the mortality curve corresponds with the peak in the concentration of lactic acid as found by Tomita. The second peak in the mortality curve coincides approximately with the pause in the growth curves. (Figs. 3 and 6.)

The chick, no doubt, passes a critical period ("metamorphosis") at this stage. This statement relating to a critical period may be substantiated by mortality data on the chick as shown in Fig. 8. The mortality is seen to pass a peak at this time. The immediate threshold mechanism causing this break in the curve at this time may be the change in the mode of respiration: the function of respiration is transferred at this time from the chorio-allantoic membrane to the lungs; that is, at this time the chick emerges from an aquatic to a terrestrial mode of respiration. But further investigations may reveal more fundamental mechanisms.

The smaller peak in the mortality curve at about five days may perhaps be correlated with the peak in the sacrolactic acid curve shown in the inset of Fig. 8. The mechanism for oxidation of lactic acid does not apparently begin to function very efficiently until this time.

Figure 9 represents the data of Hasselbalch and of Murray. The distribution of the data points is less regular in these figures than in the preceding, on account of the smaller number of embryos represented and difference in technique employed. These charts do not show the last stages of growth; otherwise, the general features of the charts are the same. The values of *k* for the data of Hasselbalch are practically the same as for the data of Atwood and Weakley. The value of *k* for Murray's data is higher, but this is probably due to a higher incubation temperature as will be demonstrated in the following paper of this series (Res. Bul. 99).

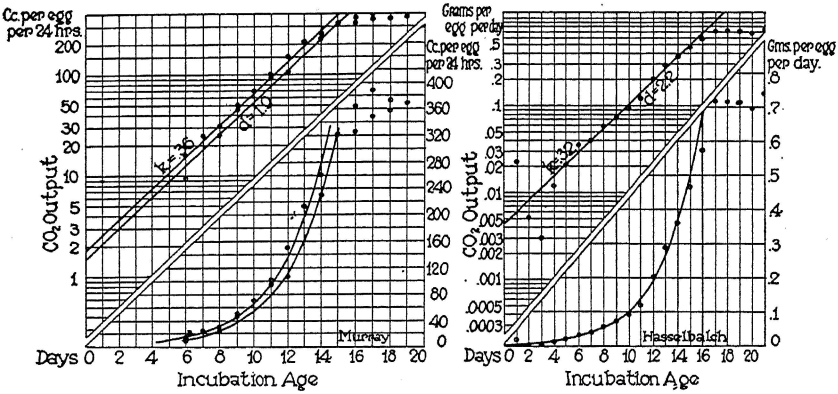

Fig. 9.—The course of carbon dioxide excretion in the chick embryo, plotted from data by Hasselbalch and by Murray.

3. Postnatal Growth in the Fowl.

3. Postnatal Growth in the Fowl.—Figure 10 represents the growth of the fowl during 12 weeks of postnatal life. There appears to be a break in the curve at 3 weeks. The major inflection occurs at the age of about 12 weeks. The values of *k* during this period are of the same order as those found for the rat.

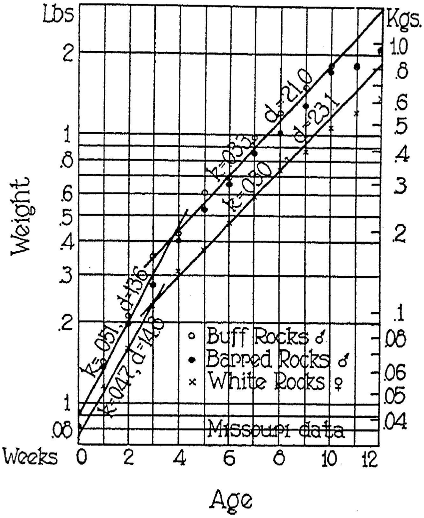

Fig. 10.—Postnatal growth of the domestic fowl during the self-accelerating phase of growth. During the first month, the rate of growth is approximately 5 per cent per day (the body weight is doubled once in 13.8 days). During the following 7 weeks, the rate of growth is approximately 3 per cent per day (the body weight is doubled once in 23.1 days).

V. GROWTH OF THE SILK WORM

Figure 11 represents the course of growth of the silk worm (Ver-a-Soie, Bombyx du Murier) as measured by the increase in nitrogen. This graph is of interest in connection with Fig. 6, indicating the course of growth in the chick embryo as measured by the increase in carbon-dioxide excretion. The two curves are remarkable for their similarity. This figure is presented here principally for its substantiating value in connection with the conception of "metamorphosis" in higher animals.

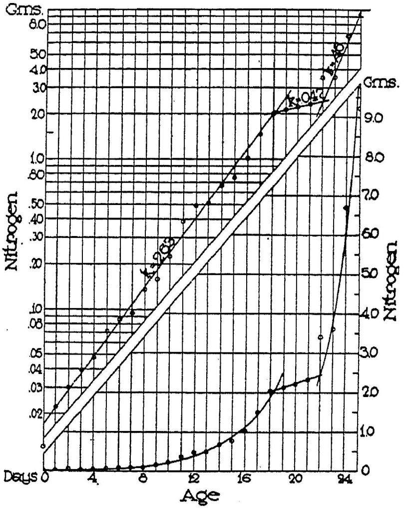

Fig. 11.—Growth of the silk worm, plotted from data by Luciani and Lo Monoco. Note the resemblance of this curve to the curve of carbon dioxide excretion in the chick embryo, shown in Fig. 6. (The values of *k* are respectively ,263 and .46.)

VI. GROWTH OF MAN

The available data on prenatal growth of man are of relatively little value from the present point of view; because, first, the ages of the specimens are not definitely known, and, second, the specimens have not all been normal. However, in view of the rather voluminous speculative literature relating to the rate of early growth in man, it seems desirable to plot some data by the method we have adopted in order to get a concrete idea as to the magnitude of the true rates of growth of the human embryo and fetus.

Figure 12 represents the data from the collection in the Carnegie Institution, published by Streeter. The striking feature of this graph is the remarkably low values for *k*. About two months after conception (the earliest age for which fairly reliable data are available), the rate of growth is only 8 per cent per day, (the body weight is doubled but once in 8.6 days); at 5 months after conception, it is only 1.7 per cent per day (the body weight is doubled once in 41 days). It will be recalled that during the week preceding birth the rat grows at 53 per cent per day, and that the lowest percentage-rate of growth in the rat, occurring shortly before puberty, is 3 per cent per day. This is a concrete illustration of the fact that given percentage-rates of growth, in different species do not signify equivalent stages of development.

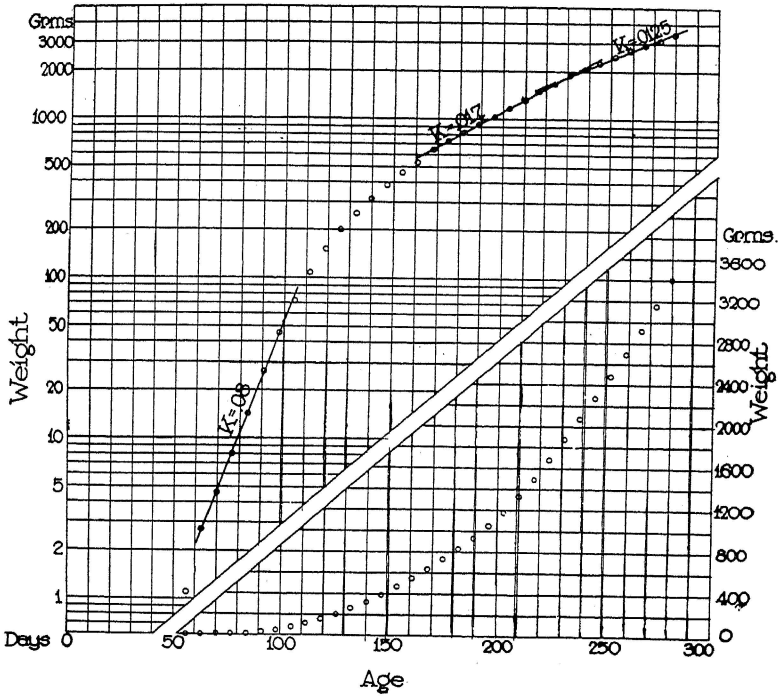

Fig. 12.—Prenatal growth in man, plotted from data published by Streeter. The values of *k* multiplied by 100 represent the instantaneous percentage-rates of growth per day. Thus during the period from 50 to 100 days of prenatal life, growth takes place at the instantaneous rate of 8 per cent per day (the body weight is doubled once in 8.7 days); between 160 and 230 days, the growth takes place at 1.7 per cent per day (the body weight is doubled once in 41 days); between 240 and 280 days, growth takes place at 1.3 per cent per day (the body weight is doubled once in 55 days). 8 per cent per day is equivalent to 240 per cent per month; 1.7 per cent per day is equivalent to 51 per cent per day; 1.25 per cent per day is equivalent to 37.5 per cent per month.

Figure 13 represents the course of growth in man between the ages of 5 and 15 years. During this period, under favorable conditions of life, growth takes place at a constant percentage-rate, of the order of 10 per cent per year, or .04 per cent per day (the body weight is doubled once in 7 years). It will be remembered that during the corresponding stages of growth in the rat, the guinea pig, and the fowl, the rate of growth is of the order of 3 per cent per day, that is, 1100 per cent per year. The percentage-rate of growth of animals is thus seen to be about 110 times as rapid as in man during the juvenile period. The fact concerning the relatively smaller rates of growth in man than in animals are not, of course, new. They were discussed at length by John Fiske and by Herbert Spencer. It is only the strictly quantitative comparisons which are new.

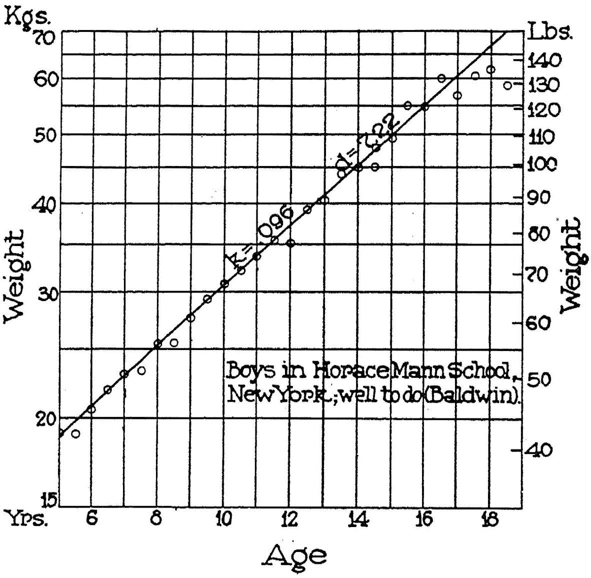

Fig. 13.—Growth in man during the juvenile period. Well nourished children grow at an approximately constant percentage-rate between 5 and 15 years (about 10 per cent per year; the body weight is doubled once in about 7 years). The so called prepubertal acceleration, so conspicuous in the literature on growth of children, is found only in the curves of poorly nourished children, as will be demonstrated in a future bulletin of this series.

The facts of growth as they relate to man are of the utmost theoretical and practical importance, and for this reason, at least one paper of this series will be devoted to the exclusive consideration of growth in man.

VII. GROWTH OF DOMESTIC MAMMALS

No data are available for prenatal growth of domestic mammals. Attempts to estimate the course of prenatal growth from the curves of increase in weight of gestating animals, have not proved successful in our work. The conclusions of Read regarding the course of growth of the fetal guinea pig based on an examination of the curve of increase in weight of the gestating mothers are, in all probability erroneous. However, data on increase in weight of gestating cattle and swine have been presented in the first paper of this series, and they may prove more useful for this purpose in the hands of others.

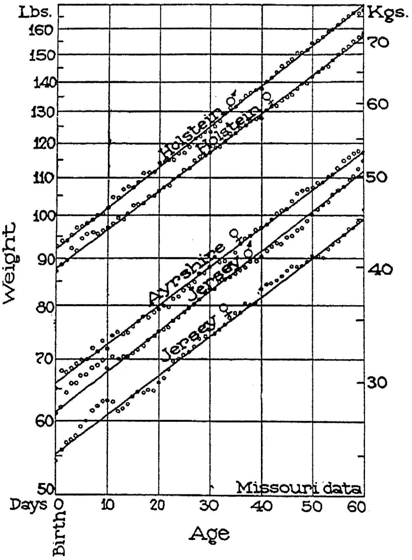

Fig. 14.—Growth of dairy cattle. During the first 60 days of postnatal life growth takes place at a constant percentage-rate (about 30 per cent per month).

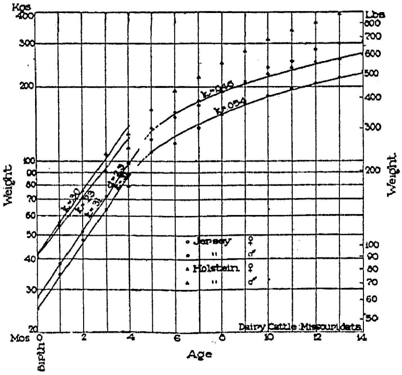

Fig. 15.—Growth of dairy cattle. The percentage-rate of growth is constant during the first four months (the rate of growth is approximately 30 per cent per month; that is, the body weight is doubled once in 2 3 months). Following the major inflection, the time-rate of growth *declines* at the rate of about 5 per cent per month.

The curves of postnatal growth of domestic animals are not entirely suitable for analysis from the point of view of the present paper for the reason that domestic animals (with the exception of the rabbit) are born at an advanced stage of development. The result is that the available segment of the curve preceding the major inflection is short, and it has a relatively small value of k. It has already been pointed out that it is not possible to ascertain definitely the "law" of growth when the relative-rate, k, falls much below 10 per cent for the unit of time under consideration. This is especially true when only a few data points are available for analysis.

However, several charts are presented in order to give some idea concerning the state of affairs as it relates to this important class of animals. Figures 14 and 15, reproduced from the first bulletin of this series, indicate that within the limitation of the present method, growth in dairy cattle takes place at a constant percentage-rate during the first four months of postnatal life. Up to 4 months, the animals grow at approximately 30 per cent per month (the weight is doubled once in about 2.3 months); after this, the time-rate of growth *declines* at about 5 per cent per month. The curve in Figure 15 is evidently not symmetrical around its center.

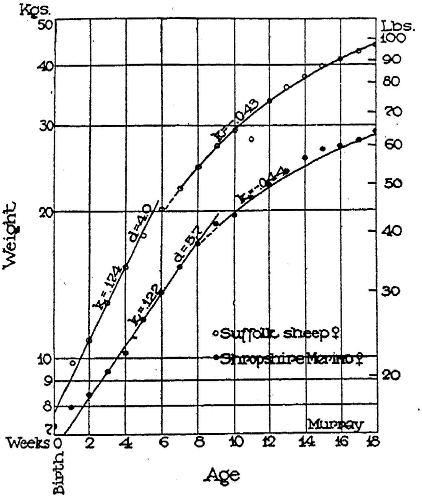

Fig. 16.—Growth of sheep. The percentage-rate of growth is constant for several weeks following birth (100 *k* represents the instantaneous percentage-rate of growth per week; *d* represents the time in weeks in which the body weight is doubled). Following the inflection, the time-rate of growth *declines* at the rate of approximately 4 per cent per week.

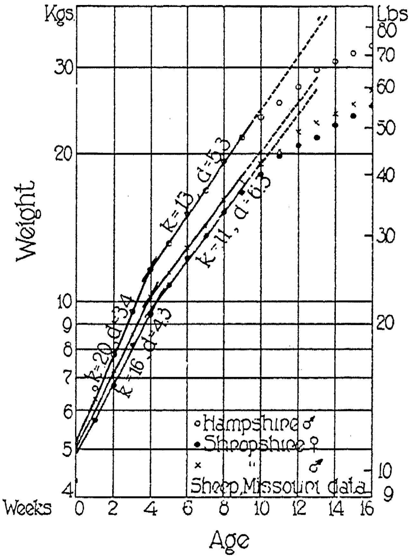

Fig. 17.—Growth of sheep. This chart indicates the presence of a break at four weeks of age. The terms *k* and *d* have the usual meaning.

Figure 16, representing growth of sheep, indicates a similar situation. Roughly, during the first two months, growth takes place at an approximately constant percentage-rate. Shropshire-Merino sheep grow at about 12 per cent per week (the body weight is doubled once in 6.0 weeks). Suffolk sheep appear to grow during this period at 17 per cent per week (the body weight is doubled once in 4 weeks). Following the inflection, the time-rate of growth *declines* at the rate of a little over 4 per cent per week. The curves are thus highly asymmetric.

Additional curves for growth in sheep are shown in Fig. 17.

The horse (*cf.* Mo. Agr. Exp. Sta. Research Bulletin 96 of this series) appears to pass the major inflection within the first four months of postnatal life.

VIII. GROWTH OF PLANTS

While this bulletin is primarily concerned with the growth of animals, it seems desirable to consider briefly a few growth curves of plants in order to render the ideas presented in these papers as general as possible.

By the way of introduction to this discussion on plant growth, it may be noted that unlike students of animal growth, plant physiologists have been more or less aware of the tendency of plants to grow exponentially. The attitude of botanists toward the problem of growth rates is not, however, unanimous. The following two quotations, one from V. H. Blackman, the leading proponent for the conception that growth is exponential, and the other from West, Briggs, and Kidd, the leading opponents of this conception, summarize the prevailing opinions on this matter:

"It is clear that in the case of an ordinary plant, the leaf area will increase as growth proceeds, and with increasing leaf area the rate of production of material by assimilation will also increase; this again will lead to a still more rapid growth and thus to a greater leaf area and a greater production of assimilating material, and so on. If the rate of assimilation per unit area of leaf surface and the rate of respiration remain constant, and the size of the leaf system bears a constant relation to the dry weight of the whole plant, then the rate of production of new material as measured by the dry weight will be proportional to the size of the plant; i. e., the plant in its increase of dry weight will follow the compound interest law. . . . .The simple equation which best applied to the growth of annual plants is thus

$$W_1 = W_0 e^{rt}$$

Where W = the final weight, W_0 = initial weight. r = the rate of interest and t = time and e is the base of natural logarithms".—Blackman, Ann. Bot. 1919, XXXIII, 353.

The above statement met with the following reply:

"A careful consideration of existing data upon plant growth does not warrant a rigid application throughout the whole life history of a plant of the compound interest conception of plant growth advocated by V. H. Blackman, and formulated by the equation

$$W_1 = W_0 \, e^{rt}$$

The value r represented by Blackman as a physiological constant and as an index of efficiency is not really constant at all in the plants which have been investigated".—West, Briggs, and Kidd, New Phytologist, 1920, XIX, 95.

The present writer's attitude toward this controversy, which still continues with full force, may be best expressed by the following fable recently retold by Graham Lusk:

> "One is reminded of the blind men of Hindustan who were taken to visit an elephant. One of them handled the trunk and found the elephant to be very like a rope; another felt the leg and found the elephant to resemble a tree, and so on.
>
> 'So these wise men of Hindustan disputed loud and long,
> Each to his own opinion exceeding stiff and strong,
> Though each was partly in the right,
> Yet all were in the wrong.' "

There is no doubt that there is a certain amount of truth in the claims of each camp. The preceding bulletin of this series (Research Bulletin 97) explained that the growth curve is sigmoid in form. During the phase of growth preceding the inflection, the larger the body, the faster it grows; but, during the phase of growth, following the inflection, the time-rate of growth decreases while the size of the organism increases. It is clear, therefore, that growth following the inflection cannot possibly take place according to the compound interest conception as proposed by Blackman; and thus far, West, Briggs, and Kidd are quite justified in their objection. Preceding the inflection, however, the rate of growth does tend to follow the compound interest principle, in plants as well as in animals; at least we hope to demonstrate to our satisfaction that it does. The evident shortcoming of Blackman's paper is the failure to indicate clearly that the compound interest conception holds only for the phase of growth preceding the inflection; also the failure to demonstrate in a convincing fashion, the applicability of this conception to data. But then, this is where the fable of the blind men of Hindustan comes in.

For the purpose of demonstrating the proposition that plants, like animals, grow in a geometric progression during the self-accelerating phase of growth, we shall treat the data on plant growth in the same manner as we have treated the data on animal growth; namely, plot the data on arithlog paper and ascertain whether the data points are distributed around a straight line.

In the examination of these curves, one must keep in mind the following differences and similarities between plants and animals: (1) even relatively slight differences in environmental temperature influence the rate of growth of plants; (2) even slight variations in light influence the rate of growth in plants; (3) the development of the seed in plants corresponds, in time, to the development of the embryo and fetus in animals. The period of germination in plants corresponds to the infantile period in animals. The period of flowering in plants corresponds to puberty in animals. The vegetative, independent growth of stem and leaves therefore corresponds to the juvenile and early adolescent phase of growth in animals.

With this introduction we may pass on to the examination of a series of growth curves of plants. Since the method of plotting for plants is the same as for animals, this matter, therefore, does not call for explanation.

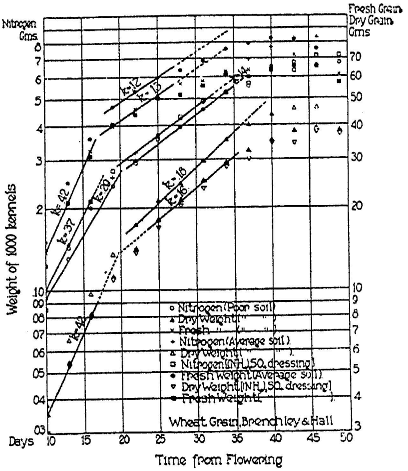

Fig. 18.—Growth of the wheat grain The terms *k* and *d* have the usual significance.

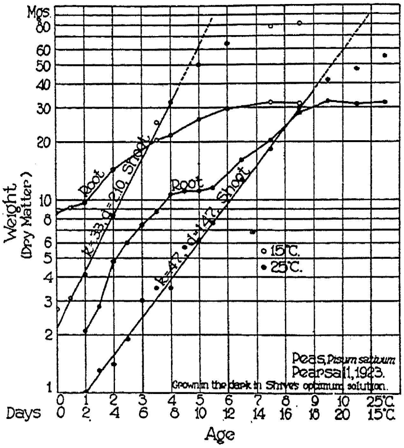

Fig. 19.—Growth of *Pisum Sativum.* The terms *k* and *d* have the usual meaning (d is the time in days in which the weight is doubled).

Figure 18 represents the growth of the wheat kernel. While the development of the seed corresponds in time to the development of the embryo and fetus in animals, it differs from the young animal in that it includes not only the embryo, but other material as well. In the ripe wheat grain, the embryo is but one-thirteenth of the weight of the kernel. A legume, such as the bean or pea, would probably be a better plant for the purpose of the present analysis. In spite of the shortcomings of the material, the distribution of the data points is quite satisfactory. The data points are distributed about straight lines in a fashion very similar to the distribution of the data points of embryonic and fetal growth in the rat, guinea pig, or fowl.

Interesting enough, there is also a relatively abrupt break in the curve. The numerical values of k, too, are of the order found in animals in the corresponding stages of development.

That this curve may suggest to the botanist an investigation of the changes in form and structure of the embryo during these stages, so as to determine precisely to what stages in animal development they might correspond.

Figure 19 represents the course of growth of the seedling, but, unfortunately, of a different plant; so it is not possible to surmise the manner of transition from the "prenatal" to the "postnatal" mode of life; not, at least, with reference to the numerical values of *k*. The numerical values of *k* are seen to be extraordinarily high during this period as compared to the value of *k* for the development of the wheat grain.

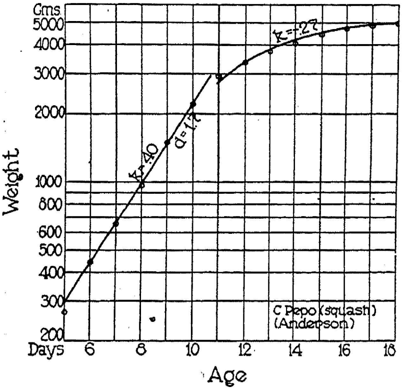

Fig 20.—The course of growth of *Cucurbita pepo* (squash). Preceding the inflection growth takes place at 40 per cent per day Following the inflection the time-rate of growth declines at the rate of 27 per cent per day.

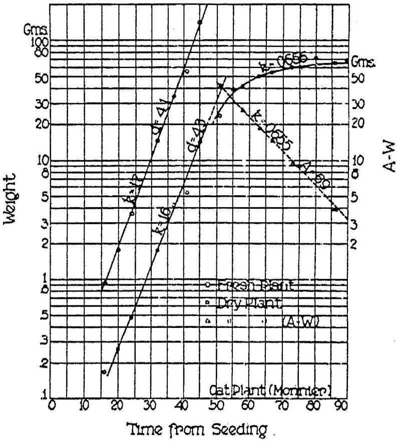

Fig. 21.—Growth of the oat plant.

Only the shoots grow exponentially. The roots appear to grow in an apparently somewhat erratic manner. The decline in the curves of the shoots at about 9 days appears to be due to a decline in food supply (the plants were grown in the dark).

Figure 20 represents the growth of the now well known *Curcurbita pepo* (squash). First Robertson, and later, Pearl, have analyzed these data.

Figure 20 shows that during the first ten days for which data are available growth in *pepo* proceeds exponentially at 40 per cent per day. Following the inflection, the time-rate of growth *declines* exponentially, at 27 per cent per day. The curve, therefore, is not symmetrical around its center. Why a fruit, the cells of which are not supposed to reproduce after the earliest stages, should grow in a geometric progression is not entirely clear.

Figure 21 indicates the course of growth of the oat plant. These data were also analyzed by Robertson (1923), and the present chart is based on the data as cited by him. This plant evidently grows at a constant percentage-rate, 17 per cent per day, until 45 days (the time of flowering); and then the time-rate of growth declines at 7 per cent per day. The curve is, therefore, not symmetrical around its center.

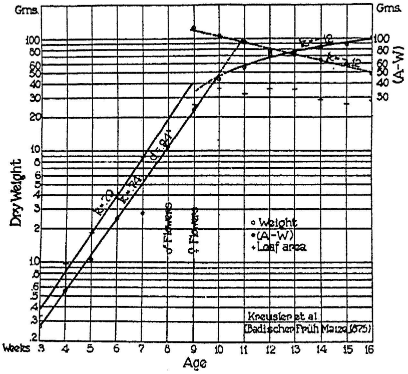

Fig. 22.—Growth of the maize plant. The terms *k* and *d* have the usual meaning. Note that the week is the unit of time in this case.

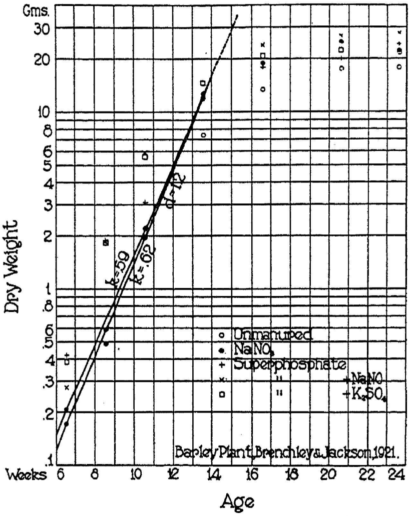

Fig. 23.—Growth of the barley plant. The terms *k* and *d* have the usual meaning, referring to the week as the unit of time.

Figure 22 represents the growth of the maize plant. The inflection occurs at the time of flowering, as is usual in all plants.

Figure 23 represents the growth of the barley plant. The data for the plants on the unmanured field, and on the field which received a dressing of sodium nitrate, are distributed around straight lines. The rate of growth is 60 per cent per day, (the weight is doubled once in 12 days). The data points for the plants grown on plots which received superphosphate, and sodium nitrate or potassium sulphate, are not distributed in so simple a manner. This is clearly due to the effect of environmental conditions.

Figures 24 and 25 represent the growth of the cotton plant in India. Inamdar and co-workers describe the climatic conditions during the season in which the observations have been made as quite variable and most unfavorable for plant growth. Considering these facts, the distribution of the data points around the straight line is quite satisfactory.

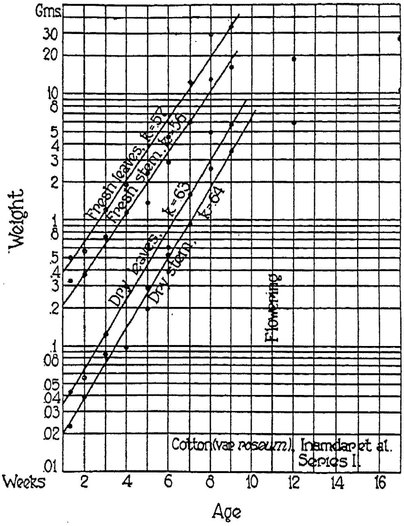

Fig. 24.—Growth of the cotton plant, Series I. The term *k* has the usual meaning referring to the week as the unit of time.

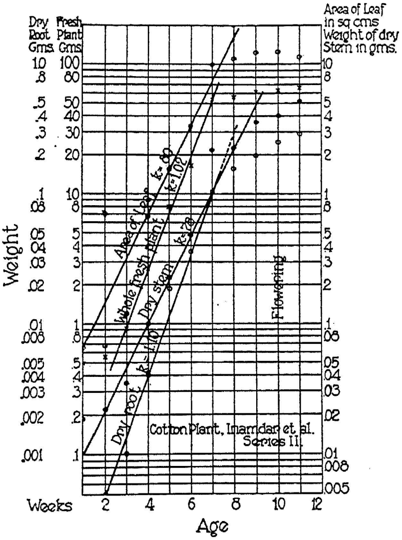

Fig. 25.—Growth of the cotton plant, Series II.

Other data are available on plant growth, which might be analyzed in the same manner (consult the bibliography of the first bulletin of this series, and particularly Brimmer, Brenchley, Briggs, Kidd, and West, Balls, Blackman, Brown, Cambage, Fittbogen, Gericke, Gressler, Gregory, Hornberger, Hackenberg, Hanzlik, Kreussler, Mason, Monnier, Mutschler, Moritz, Newbauer, Osswald, Patton, Priestly, Presscott, Wildt); but the illustrations presented in this section are probably sufficiently convincing of the general thesis that early growth in plants, like growth in animals, is exponential. There is an urgent need, however, for data of a suitable plant, preferably a legume (the seed of which is made up largely of embryo), representing the whole life-history of the same plant as grown under optimum natural conditions. These data should include daily measurements of the developing seed from the earliest stages, continuing through the periods of germination, independent vegetative growth, reproduction and senescence (these stages corresponding respectively to the periods of prenatal, infantile, juvenile, and adolescent growth, and senescence in animals). The data discussed in this bulletin have the fault of presenting the several stages of growth on *different* plants, including the development of a seed, the embryo of which constitutes but a small fraction of the seed; the germination of another seed in the *dark*, and finally the vegetative and reproductive periods of still other plants grown under highly variable field conditions. These data do not throw light on the nature of the several transition stages—the transition, for example, from the period of germination (corresponding to the infantile period in animals) to the independent vegetative growth (corresponding to the juvenile phase in animals).

IX. GROWTH OF POPULATIONS

It was pointed out in the preceding bulletin of this series that the process of growth in size, in a multicellular organism is similar in nature to the growth in size of a population of organisms in a finite universe; also that the general mechanisms of growth are the same in both cases, and that, therefore, the general shapes of the growth curves are the same in both cases. This conception of essential similarity between the two types of growth was illustrated by means of growth curves of human and bacterial populations. In order to give symmetry to this discussion and to keep before the mind the generality of the conceptions underlying this series of papers, it seems desirable, before closing, to present several growth curves of populations.

Figure 27 represents the growth of populations of bacteria at various temperatures. Figure 28 represents the growth of populations of soil algae under several different environmental conditions. The data points are evidently distributed in a satisfactory manner around the straight lines, thus indicating the essential similarity between growth of populations and of multicellular organisms during the self-accelerating phase of growth.

To avoid misunderstanding, it is necessary to point out that students of growth of populations of micro-organisms—or at least Lane-Claypon and Roach, have been quite aware of the exponential nature of growth of populations in their early history. Both of these investigators have plotted the logarithms of their data and found them distributed about straight lines within the limits indicated in Figs. 26 and 27. What we have done, is to plot these values on arithlog paper and to give concrete meaning to the slopes of these curves; *k*, representing the slope of the curve, is the instantaneous percentage-rate of growth for the unit of time under consideration indicated on the axis of abcissae. Thus, *B. Coli* at 42°C. grows at the instantaneous rate of 217 per cent per hour; that is, the size of the population is doubled once in $\frac{.693}{2.17} = .32$ hour, or 19 minutes.

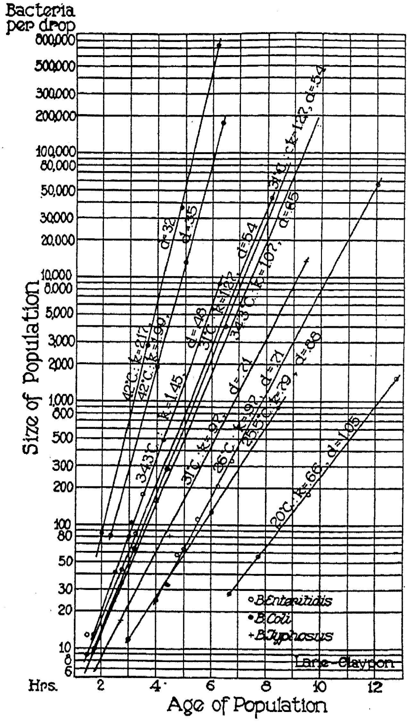

Fig. 26.—Growth of bacteria at various temperatures. The expression 100 *k* represents the instantaneous percentage-rate of growth per hour. *d* represents the time in hours in which the population is doubled. A change in temperature within the given limits does not change the form of the curves; it merely changes the slope of the curve.

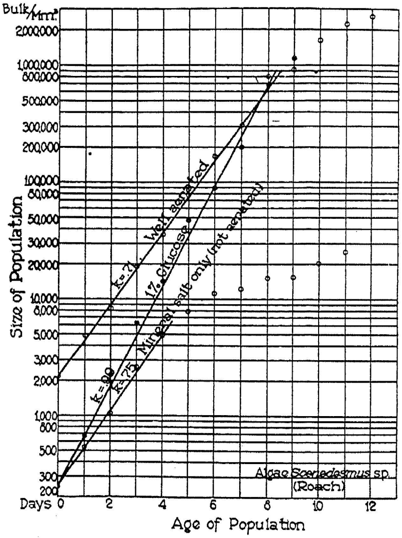

Fig. 27.—Growth of populations of soil algae. The term *k* has the usual meaning. The environmental conditions within the given limits change the slope of the curves but not their shape.

X. SUMMARY AND CONCLUSIONS

The present bulletin is merely an extension of the preceding one (Research Bulletin 97) in this series. Its purpose is to demonstrate in some detail the statements made in the preceding bulletin relating to growth rates during the phase of growth preceding the major inflection.

It is believed that the following statements made in the preceding bulletin were substantiated:

1. Growth preceding the major inflections is, in multicellular organisms, a discontinuous process. In the curves of animals examined, there are at least four breaks in the curve during this phase of growth. In the higher plants examined there are at least three breaks in the curve; however, the available data for plant growth are less adequate than for animal growth, and we are, therefore, less certain of this conclusion as it relates to plants.

2. The percentage-rates of growth between successive breaks in the curve are, within the limits of experimental error, constant.

3. The inherent, or initial, instantaneous percentage-rates of growth in warm-blooded animals are of the order of 100-200 per cent per day.

4. Curves of population growth resemble, in their general features curves of growth of individual multicellular organisms. However, the abrupt breaks in the segments preceding the major inflection, which form so conspicuous a feature in the growth curves of multicellular animals, do not appear to be present, or at least they are not constant, or necessary, features of the curves of population growth.

5. The numerical values for instantaneous relative-rates of growth are given in the charts or in the legends to the charts. The highest rate encountered was for the growth of *B. Coli* at 42°C. The population of *B. Coli* under these conditions grows at 217 per cent per hour; that is, the population is doubled every 19 minutes. The domestic fowl appears to begin growth at the rate of 100 per cent per day (the weight is doubled once in .7 day or 17 hours). During the nine days preceding birth, the rat grows at the rate of 53 per cent per day (the body weight is doubled once in 1.3 days). Man at the corresponding age grows at 1.7 per cent per day (the body weight is doubled but once in 41 days). It appears that the most rapid rates of growth are found in the most primitive forms (bacteria), and the slowest rates of growth are found in the most evolved form (man). It may be mentioned that recent investigations indicate that bacteriophage develop more rapidy than bacteria.

SOURCES OF DATA AND BIBLIOGRAPHY

The sources of data are indicated either on the chart, or in the legend for the chart. The charts labelled "Missouri Data", are based on the data presented by their authors (or representatives of the authors) in the first (cooperative) bulletin (Research Bulletin 96) of this series. The reader must be referred to that bulletin for detailed credit to the investigators participating in the work, or making the measurements. In other cases, the author's name is indicated, and the reference to the original paper may be found in the bibliography of that bulletin.

ADDENDUM

Since this manuscript was submitted for publication, the writer had the privilege of discussing the mortality curve of the chick embryo (Fig. 8) with Dr. C. R. Stockard of the Cornell University Medical School. Dr. Stockard called attention to the fact that the peak in the mortality curve of the chick at 5 days corresponds to the similar peak in the prenatal mortality curve of man at 3 months. This represents the junction between the embryonic period (formation of organs) and the fetal period (enlargement of organs). According to Dr. Stockard the character of growth in the two periods of growth is quite different, and that it is consequently not at all surprising to find a high mortality (and a break in the growth curve) at this time.