SPECIAL ARTICLES

THE SHAPE OF THE CHICK EMBRYO GROWTH CURVE[1]

MURRAY[2] has found that the logarithm of the chick embryo weight when plotted against the logarithm of age yields a straight line from 5 to 19 days of age. Although he did not attach any significance to this observation, some of the later investigators, who apparently have confirmed Murray's finding, have on basis of it elaborated several different hypotheses regarding the nature of the growth process. Needham[3] in his exhaustive treatise on chemical embryology reviewed these adequately, and it is not necessary for the purpose of this note to reiterate any of them. It may be, however, mentioned that a recent generalization of the laws of growth (Glaser[4]) also utilizes Murray's observation.

It is obvious that, if chick embryo growth conforms to a single logarithmic straight line throughout the embryonic period, far-reaching consequences for generalized descriptions of the growth process may ensue. It is therefore exceedingly important to determine the validity of describing the total chick embryo growth by means of such a straight line.

In preparing a logarithmic plot of unpublished data from this laboratory, it was noted that while an excellent straight line fit was obtained for the portion of the growth curve from 7 to 12 days of age, a flexure was noted at about 12 days. The observed weights rose above the calculated ones, the difference between the two gradually disappearing towards the end of the embryonic life of the chick.

Fortunately, Needham (Appendix I, Table 3) lists a number of sets of embryo weights obtained by various investigators, thus affording an opportunity to examine these sets for similar deviations. The more complete sets comprising the data of Falck, Hasselbach (two sets), Bohr and Hasselbach, Lamson and Edmond, Iljin, Schmalhausen (two sets), Henderson and Brody, Romanoff, and Byerly (loc. of all cited by Needham) were thus utilized. Murray's data were obtained from his original paper, since Needham cites the calculated rather than the observed figures. In addition the data presented by Landauer[5] for normal embryos and the data from this laboratory[6] were used.

The procedure was to obtain the least squares fit to the straight line

$$\log w = a \log t + b$$

for each of the sets for the period from 7 to 12 days of age. If the straight line fit is legitimate for the whole of the embryonic growth period, the equation obtained on basis of these six points should apply equally well to the period from 12 to 20 days. Calculated logarithms of weights for each age from 7 to 20 days were then obtained and the deviations from the observed logarithms of weights computed. In each case the origin of the deviations may be considered as the straight line resulting from a plot of calculated log weights against themselves. The slope of this line is equal to unity in all the sets. This permits calculation of the mean deviation with its standard error for each day of incubation.

It should be noted that the first four sets cited were recorded in 1900 and earlier. The conditions of incubation under which the embryos were grown were probably not optimum, since great advances in incubation technique have been made since that time. This fact would undoubtedly tend to distort the normal progress of growth, and because of it computations are presented both including and excluding these four sets. Thus for the first computation 14 sets of data were used, while for the second only 10. These numbers varied somewhat, since not all ages are represented in all the sets of data.

Table 1 presents the mean deviations for each age.

TABLE 1

DEVIATION OF OBSERVED FROM CALCULATED LOGARITHMS OF EMBRYO WEIGHT

	All data (14 sets)		Data since 1900 (10 sets)	
Age	Mean deviation	Dev./S.E.	Mean deviation	Dev./S.E.
7 ..	.0009 ± .0057	.16	−.0006 ± .0055	.11
8 ..	.0036 ± .0088	.41	.0038 ± .0050	.76
9 ..	.0003 ± .0108	.03	.0046 ± .0115	.40
10 ..	.0076 ± .0096	.79	.0014 ± .0063	.22
11 ..	−.0049 ± .0132	.37	−.0053 ± .0121	.44
12 ..	−.0144 ± .0062	2.32	−.0066 ± .0044	1.50
13 ..	.0231 ± .0143	1.62	.0424 ± .0102	4.16
14 ..	.0376 ± .0133	2.83	.0527 ± .0112	4.71
15 ..	.0290 ± .0175	1.66	.0500 ± .0115	4.35
16 ..	.0278 ± .0201	1.38	.0468 ± .0173	2.71
17 ..	.0108 ± .0217	.50	.0405 ± .0157	2.58
18 ..	−.0075 ± .0268	.28	.0242 ± .0253	.96
19 ..	.0075 ± .0224	.33	.0169 ± .0225	.75
20 ..	.0061 ± .0270	.23	.0104 ± .0298	.35

The first series of computations indicate significant deviations only at 12 and at 14 days of age. It is, however, the second series that brings out the fact that the deviations observed originally in the data from this laboratory were not chance fluctuations. There appears to be a sharp acceleration in the observed growth at 13 days of age. The discrepancies between the observed and calculated logarithms of embryo weight rise to a maximum at 14 days and then grad-

[1] Assistance in computations was provided under WPA project A. P. No. 465-03-3-209.

[2] H. A. Murray, Jr., *Jour. Gen. Physiol.*, 9: 39, 1925.

[3] J. Needham, "Chemical Embryology," 3 vols. Cambridge University Press, 1931.

[4] O. Glaser, *Biol. Rev.*, 13: 20, 1938.

[5] W. Landauer, *Storrs Agr. Exp. Sta. Bull.*, 193, 1934.

[6] I. M. Lerner and C. A. Gunns. Unpublished, 1938.

ually decrease until they lose their statistical significance at 18 days of age. There remains but little doubt of the reality of these deviations, and the conclusion that a single straight line does not fit the whole period of embryonic growth seems unescapable.

It is of interest to note that a similar picture prevails in embryos incubated under the high temperature of 105° F. as revealed by similar computations involving the data of Henderson and Brody.[7] However, here the acceleration occurs at an earlier stage, which is, perhaps, in keeping with the usual temperature effects on rates of processes. The fragmentary data of the same workers on embryos incubated at 95° F. reveal a complete distortion of the logarithmic straight line. These observations lend support to the legitimacy of disregarding the data of the earlier workers.

The significance of the finding here reported undoubtedly needs further elaboration and explanation in biochemical terms. Thus the curve of log dry weight plotted against log time, presented graphically by Glaser from Murray's[8] data, shows a very pronounced flexure of the same type as observed here. The differentiation of energy sources during the course of embryonic growth (Needham, p. 992) may also be recalled in this connection, as may also fluctuations in glutathione concentration (Gregory, Asmundson and Goss[9]).

The purpose of this note, however, is limited to drawing attention to the fact that while individual sets of data may produce a satisfactory fit to the logarithmic straight line, small deviations in the same direction and appearing at the same time in the majority of sets of reliable data can not be disregarded. Cognizance of this situation is commended to workers in the field of embryonic growth.

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THE ROLE OF HEREDITY VERSUS ENVIRONMENT IN LIMB BUD TRANSPLANTS BETWEEN DIFFERENT BREEDS OF FOWL

USING the technique developed by Hamburger,[1] the author has transplanted 60- to 70-hour White Leghorn limb buds into the coelome of Brown Leghorn hosts of the same age. The host embryos were then allowed to develop until 15 or more days of age. Two different types of results have been obtained. In seven cases in which the grafts became attached to the mesenteries, a normal White Leghorn leg developed upon the Brown Leghorn host. The feathers of the transplant were white, and the scales on the shank and foot were characteristically pigmented. The White Leghorn graft, therefore, differentiated according to its hereditary potentialities. The environment, in these cases, seemed to have had no influence.

These results are at variance with those of Willier and his co-workers, who have reported[2] that White Leghorn limb buds developed colored plumage when grafted to colored breeds. Two grafts, however, have been obtained which seem to clarify this discrepancy. In one case the graft possessed Brown Leghorn feathers and the scales of the shank were pigmented, while the foot had yellow scales typical of the White Leghorn. In this instance environmental influences have been able to suppress, almost completely, the hereditary potentialities of the graft. In another the upper part of the leg was covered with brown feathers, the lower portion with white, and the shank and foot were unpigmented. This case, therefore, was an intergrade. Both these latter grafts were exceedingly well attached to the inner body wall.

These results indicate that White Leghorn plumage develops on grafts which are attached to the mesenteries and that Brown Leghorn plumage occurs on grafts that are attached to the body wall. It is possible that the results may be explained on the basis of a diffusion gradient between host and graft. If the graft is well attached to the host and an enzyme or "color-inducing substance" reaches the transplant in sufficient amounts, the hereditary potentialities of the graft are suppressed completely and the transplant develops the plumage and pigmentation characteristic of the host. If the attachment is less secure and a smaller amount of color-inducing substance reaches the graft, an intergrade results. In cases where little or no enzyme diffuses into the graft, a typical White Leghorn leg develops on the brown host. A further analysis of this problem is in progress.

In reciprocal transplants, Brown Leghorn limb buds transplanted to White Leghorn hosts, three different types of results were obtained. In several cases typical Brown Leghorn feathers developed upon the transplanted limb, and the shank and foot possessed the typical pigmentation of the Brown Leghorn. These results confirm the findings of Willier, who obtained similar results with skin grafts. In three cases the environment has suppressed, or at least retarded, the development of the brown feathers since 15-day-old transplants possessed all white feathers or else only a few feathers were pigmented.

[7] E. W. Henderson and S. Brody, *Mo. Agr. Exp. Sta. Res. Bull.*, 99, 1927.
[8] H. A. Murray, Jr., *Jour. Gen. Physiol.*, 9: 405, 1926.
[9] P. W. Gregory, V. S. Asmundson and H. Goss, *Jour. Exp. Zool.*, 73: 263, 1936.
[1] Viktor Hamburger, *Jour. Exp. Zool.*, 77: 379–399, 1938.
[2] B. H. Willier, Mary E. Rawles and E. Hadorn, *Proc. Nat. Acad. Sci.*, 23: 542–546, 1937.