

## Genetical studies on growth and form in the fowl

### 1. PHENOTYPIC VARIATION IN THE RELATIVE GROWTH PATTERN OF SHANK LENGTH AND BODY-WEIGHT

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*(Received 15 June 1962)*

The shape or form of the animal body can, with certain limitations (Medawar, 1945), be regarded as a metrical quantitative character. It is also one which undergoes considerable changes during evolution and during individual ontogeny; growth usually involves changes in shape as well as increase in mere size. Yet there is remarkably little information linking these two aspects of form—the genetic and the ontogenetic—to each other.

The experiments to be reported in this and subsequent papers are intended to study the response to selection for a criterion of metrical form, with particular reference to the ontogenesis of the changes produced by selection. The complexities of analysing multivariate data dictated the choice of a simple measure of form, using only two measurements. Shank length and body-weight have been chosen for a number of reasons. They may be measured rapidly and with reasonable accuracy on live birds, and the early work of Lerner (1937) and Jaap (1943) suggested that they would yield an approximately linear allometric relation (Reeve & Huxley, 1945) over the major part of post-natal growth, and so facilitate analysis in a way which expresses changes in shape directly in terms of relative growth rates. Finally, their relation is one which is likely to have an important bearing on the table qualities of chickens: for a given body-weight a shorter shank is likely to reflect, at least in part, a more plumply fleshed body. A third measurement, shank width, has been used as an ancillary, to provide some indication of the anatomical nature of variations in the shank length : body-weight relation.

We shall be concerned here solely with an analysis of phenotypic variation in the populations used as the starting point of the selection experiments. This was an essential preliminary to the formulation of a criterion of selection, and to the study of the genetic changes produced by selection, which will be dealt with in other papers. Fuller details of procedures and results have been given elsewhere (Cock, 1962).

## 1. MATERIAL, MANAGEMENT AND MEASUREMENTS

The data consist of measurements of body-weight, shank length and shank width at ages from 2 to 52 weeks (counted from the date of hatching) on two  $F_1$  breed crosses: Indian Game (Dark Cornish) ♂ × Light Sussex ♀ and White Leghorn × Rhode Island Red. These breeds will be referred to by the following symbols:

G = Indian Game

S = Light Sussex

L = White Leghorn

R = Rhode Island Red

so that the two crosses are  $G \times S$  and  $L \times R$ ; they are unpedigreed stock, bought in as hatching eggs from commercial breeders, and hatched simultaneously on 5th September, 1958. They have since been crossed together to form a base population for the selection experiments, and the four breeds were deliberately chosen with a view to introducing a wide range of variation in adult size and conformation. With the proviso that characterization of breeds is at best an approximate matter, the breeds would form a series L, R, S, G in ascending order of plumpness of fleshing and stockiness of general build; in adult body-weight they rank in the same ascending order.

The chicks were reared in battery brooders up to 7 weeks, and later in floor pens and individual cages.  $G \times S$  and  $L \times R$  were kept in separate, but similar and adjoining, compartments, but the sexes were intermingled until 14 weeks. The data up to 23 weeks relate to a total of 158 birds. Restricted samples only (81 birds) were retained and measured beyond this age to 52 weeks. The entire records of all birds dying up to 52 weeks, and of one bird which temporarily lost weight between 9 and 10 weeks (24 birds in all), have been excluded. Body-weights were recorded to the nearest g. up to 200 g., to the nearest 5 g. up to 1000 g., and to the nearest 10 g. above 1000 g. Shank length was measured to the nearest millimetre; in all essentials the method of measurement is the same as that recommended by Lerner & Burmester (1937), save that ordinary parallel-jaw callipers are used, instead of a special apparatus. The leg is held so that the tarsal joint and the joint between the tarsometatarsus and the middle toe both form right angles, and the callipers are applied to measure the distance between the centre of the foot-pad and the posterior surface of the tarsal joint. The measurement thus includes (besides overlying soft tissues, which constitute 5% or less of the whole) the length of the tarsometatarsus plus the thickness of the distal head of the tibiotarsus. Shank width was measured with vernier callipers as the transverse width at the narrowest part of the shank—assessed visually, and normally about half-way down the shank. Shank width was not measured before 8 weeks of age, and the 8-, 10- and 12-week measurements were recorded to the nearest 0.5 mm.; later measurements all to the nearest 0.1 mm. In both length and width, only one shank (the right) was measured. All measurements and weighings were made by the author throughout.

## 2. TERMINOLOGY AND STATISTICAL TREATMENT

The present data are, in the usual terminology of growth studies (Tanner, 1951; 1962), *longitudinal*; i.e. exactly the same set of individuals has been measured at each age, so that each individual is followed *along* the course of its growth. The contrasting category of data is *cross-sectional*, in which an entirely different sample (cross-section) of the population is measured at each age. A third category of data—*static*—arises only when two or more measurements are involved (i.e. shape as well as size is being studied), and was therefore not defined by Tanner. Static data consist of one set of measurements made on individuals all of the same age; the term *static* is used because such data yield information on size and shape at a given age, but not on the dynamic (growth) processes by which this is reached. Cross-sectional data consist of an age-series of sets of static data, each obtained from a different sample; longitudinal data consist of a similar series all based on the same sample.

These three types of data form a hierarchy; longitudinal data can yield all the types of information obtainable from cross-sectional or static data and, in addition information (on individual variation in growth characteristics) obtainable only from longitudinal data. Similarly, cross-sectional data can yield information (on the *average* growth characteristics of the population) additional to that also obtainable from static data. Each type of data needs its own appropriate type of analysis; it is convenient to apply the same terms—longitudinal, cross-sectional and static—to the types of analysis. Because of the hierarchical relation between the kinds of data, a complete analysis of a set of longitudinal data involves all three types of analysis.

Although (since the present data are in fact longitudinal) only the longitudinal type of analysis is competent to yield valid significance tests of population differences in growth characteristics, such an analysis is computationally laborious, and it has been practicable to apply it only to that part of the growth curve representable by a straight line (Section 4). The general features of the growth curves, over the entire period for which data have been collected, have therefore been dealt with by cross-sectional analysis only (Section 3). The present data are regarded partly as an illustrative example of the potentialities of complete analysis of longitudinal data. Since there appears to be no published concrete example of such analysis (except for a single measurement only—see Tanner, 1951; 1962) a partial static analysis (at one age only) is also given (Section 5).

All weights and measurements have been transformed initially to base 10 logarithms (three places of decimals) and all computations carried out on the transformed data. The actual weights, shank lengths and shank widths will be denoted by  $X$ ,  $Y$  and  $Z$  respectively, and the corresponding small letters will be used for their logarithms. Thus:

$$\begin{aligned}x &= \log_{10} X; & X &= \text{body-weight in g.} \\y &= \log_{10} Y; & Y &= \text{shank length in cm.} \\z &= \log_{10} Z; & Z &= \text{shank width in mm.}\end{aligned}$$

We shall be dealing with values of  $x$ ,  $y$  and  $z$  both at different ages in the same individual and in different individuals. A group will comprise all the individuals

of the same sex and cross, and the number of individuals in a group will be denoted by  $N$ . The number of ages for each individual will be denoted by  $n$ . Where necessary to avoid ambiguity, the individual and age concerned will be indicated by suffixes;  $x_{it}$  will denote the (observed) value of  $x$  in the  $i$ th member of the group at  $t$  weeks of age, and similarly for  $y$  and  $z$ . The following terminology will be adopted for means:

$$\left. \begin{aligned} \bar{x}_i &= \frac{1}{n} \sum_{t=1}^n x_{it}; & \bar{x}_t &= \frac{1}{N} \sum_{i=1}^N x_{it}; \\ \bar{\bar{x}} &= \frac{1}{N} \sum_{i=1}^N \bar{x}_i = \frac{1}{n} \sum_{t=1}^n \bar{x}_t, \end{aligned} \right\} \tag{1}$$

and similarly for  $y$  and  $z$ . Suffixes and bars will, however, be omitted when the meaning is already clear from the context.

The analysis adopted consists essentially of the calculation of simple linear regression equations of  $y$  on  $x$  and of  $z$  on  $x$ . The sum of squares of deviations of  $x_{it}$  ( $t = 1 \dots n$ ) about  $\bar{x}_i$  will be denoted by  $S_i(x^2)$  and the corresponding variance ( $S_i(x^2)/n - 1$ ) by  $\text{var}(x)$ , with a similar usage for other summations and variables;  $\text{cov}(xy)$  will be used for covariances. The regression coefficient of  $y$  on  $x$  (or of  $z$  on  $x$ ) will be denoted by  $k$ . Because of the bias inherent in  $k$  (due to the fact that  $x$  is arbitrarily taken as the independent variable) the estimate recommended by Teissier (1948) and by Kermack & Haldane (1950) will also be given: this will be denoted by  $k'$ . The coefficient of correlation between  $x$  and  $y$  will be denoted by  $r$ , and the sum of squares of deviations of  $y$  about the regression line will be denoted by  $S(d^2)$ . With these definitions the usual regression formulae become:

$$\left. \begin{aligned} k &= \frac{S(xy)}{S(x^2)}; & k' &= \left[ \frac{S(y)^2}{S(x)^2} \right]^{\frac{1}{2}} = \frac{k}{r}; \\ S(d^2) &= \left[ S(y^2) - \frac{S^2(xy)}{S(x^2)} \right]; & \text{var}(d) &= \frac{S(d^2)}{n-2}; \\ \text{error variance of } k \text{ or } k' &= \text{var}_{\mathbb{E}}(k) = \frac{\text{var}(d)}{S(x^2)}; \\ \text{regression estimate of } y \text{ at } (x = \bar{x} + a) &= \hat{y}_a = \bar{y} + ak; \\ \text{error variance of } \hat{y}_a &= \text{var}_{\mathbb{E}}(\hat{y}_a) = \frac{\text{var}(d)}{n} + a^2 \text{var}_{\mathbb{E}}(k) \end{aligned} \right\} \tag{2}$$

Although the algebraic suffix  $a$  to  $\hat{y}$  is measured from  $x$ , numerical suffixes to  $\hat{y}$  (and the algebraic suffix  $x$  itself) will be measured from the origin. (This convention is introduced to avoid the use of multi-digit suffixes.) Suffixes  $y$  or  $z$  will be added, where necessary, to  $k$ ,  $k'$  and  $d$ , to indicate whether the regression of  $y$  or of  $z$  on  $x$  is involved.

The formulae (2) as given, with  $x$ ,  $S(x^2)$ , etc., interpreted as  $x_i$ ,  $S_i(x^2)$ , etc., are appropriate to the calculation of the regression line for the successive pairs of measurements made on a single individual (longitudinal analysis). In calculating

the regression for group means at different ages (cross-sectional analysis),  $\bar{x}_t$  and  $\bar{y}_t$  replace  $x$  and  $y$ , and  $\bar{x}$  and  $\bar{y}$  replace  $\bar{x}$  and  $\bar{y}$ . For static analysis  $x$ ,  $S(x^2)$ , etc. are interpreted as  $\bar{x}_t$ ,  $S_t(x^2)$ , etc., and  $N$  replaces  $n$ .

The parameter  $k$  (or  $k'$ ) is, biologically, a coefficient of allometry. The term allometry covers two quite distinct phenomena; *heterauxesis* and *allomorphosis* (Reeve & Huxley, 1945). A  $k$  obtained from longitudinal or cross-sectional analysis represents a coefficient of heterauxesis. It will here be termed a *coefficient of longitudinal* or *cross-sectional allometry*, and denoted by  $k_L$  or  $k_C$ . To indicate  $k_L$  or  $k_C$  indifferently, *coefficient of ontogenetic allometry*, or *relative growth rate*, and  $k_o$  will be used. There is a close relationship, mathematical as well as biological between  $k_L$  and  $k_C$ . Where, as in the present data, the fit to the allometry equation is good,  $k_C$  and the mean of the  $k_L$  values obtained from the same data are practically identical (see Sections 3 and 4). A coefficient obtained from static analysis ( $k_S$ ; *coefficient of static allometry*), on the other hand, corresponds to a coefficient of allomorphosis. (The various kinds of suffix may be combined; thus  $k_{Syt}$  denotes the coefficient of static allometry of  $y$  relative to  $x$  at  $t$  weeks of age.) The term 'relative growth rate' cannot properly be applied to  $k_S$ , since the data on which it is based are obtained all at one age, and thus contain information on the results of growth, but not on growth itself (Reeve & Huxley, 1945; Richards & Kavanagh, 1945). There is no reason, biological or mathematical, why the numerical values of  $k_o$  and  $k_S$  derived from the same data should be similar (see Section 5 for an example).

As a general rule (again exemplified by the present data: see Sections 4 and 5), the fit to the allometry equation will be good (i.e.  $r$  will be high) in deriving  $k_o$ , and the numerical values of  $k_o$  and  $k'_o$  will therefore be nearly identical. In deriving  $k_S$ , on the other hand, the fit will usually be much poorer ( $r$  will be low), and  $k_S$  and  $k'_S$  will correspondingly differ widely.

### 3. CROSS-SECTIONAL ANALYSIS: GENERAL CHARACTERISTICS OF THE GROUP ALLOMETRY CURVES

#### (i) *The shank length: body-weight curves*

The means ( $\bar{x}_t$  and  $\bar{y}_t$ ) up to 23 weeks are plotted for each group in Figs. 1 and 2. Regression lines based on the 2–10-week measurements have been fitted to the plots; the parameters of the regression equations are given in Table 1 (a). Deviations at each age of the actual from the calculated values ( $\hat{y}$ ) are given in Table 2. The standard errors given for  $k_y$  and  $\hat{y}_{2.75}$  in Table 1 (and for  $k_z$  and  $\hat{z}_{3.1}$ : see Section 3 (b)) are not strictly appropriate for testing the significance of group differences (although they would be appropriate if the data were cross-sectional). The appropriate standard errors are those derived from longitudinal analysis, which are given in Table 7. These are, in the case of  $k_y$ , smaller by factors of 2 to 3 than the cross-sectional standard errors of Table 1. In the case of  $\hat{y}_{2.75}$  (cross-sectional standard errors for  $\hat{y}_{2.75}$  and  $\hat{y}_{\bar{x}}$  are identical to the number of decimal places given) the cross-sectional and longitudinal standard errors are of very similar magnitude, while for

$\hat{z}_{3.1}$  the longitudinal standard errors are larger by factors of up to 2. In the present data use of the cross-sectional standard errors does not (except in one minor respect noted below) lead to misleading conclusions as to the significance of group differences. (The relative magnitude of longitudinal and cross-sectional standard errors depends on the number and variability of the individuals in the group, the number of ages measured and the closeness of fit of the cross-sectional regression. In other

Table 1. Regression parameters from cross-sectional analysis

Number of individuals ( $N$ )	G $\times$ S $\delta\delta$ 38	G $\times$ S $\varphi\varphi$ 27	L $\times$ R $\delta\delta$ 47	L $\times$ R $\varphi\varphi$ 46
(a) $\bar{y}$ on $\bar{x}$ ; 2-10 weeks ( $n = 9$ )				
$k_{Cy}$	0.3897 $\pm$ 0.0036	0.3841 $\pm$ 0.0046	0.4072 $\pm$ 0.0050	0.4033 $\pm$ 0.0041
$k'_{Cy}$	0.3899	0.3843	0.4074	0.4035
$\bar{x}$	2.7946	2.7348	2.7619	2.7065
$\bar{y}$	0.8807	0.8645	0.8851	0.8549
$\hat{y}_{2.75}$	0.8633 $\pm$ 0.0011	0.8523 $\pm$ 0.0013	0.8802 $\pm$ 0.0014	0.8724 $\pm$ 0.0011
var( $d$ )	$10.7 \times 10^{-6}$	$15.6 \times 10^{-6}$	$17.2 \times 10^{-6}$	$10.8 \times 10^{-6}$
(b) $\bar{z}$ on $\bar{x}$ ; 8-17 weeks ( $n = 5$ )				
$k_{Cz}$	0.238 $\pm$ 0.010	0.188 $\pm$ 0.018	0.274 $\pm$ 0.012	0.258 $\pm$ 0.010
$k'_{Cz}$	0.239	0.190	0.275	0.258
$\bar{x}$	3.2475	3.1395	3.1967	3.0985
$\bar{z}$	1.0492	0.9963	1.0030	0.9471
$\hat{z}_{3.1}$	1.0141 $\pm$ 0.0019	0.9889 $\pm$ 0.0021	0.9763 $\pm$ 0.0020	0.9475 $\pm$ 0.0011
var( $d$ )	$8.3 \times 10^{-6}$	$19.3 \times 10^{-6}$	$13.0 \times 10^{-6}$	$6.3 \times 10^{-6}$

Var( $d$ ) and the standard errors of  $k$ ,  $\hat{y}$  and  $\hat{z}$  have  $n - 2$  degrees of freedom. Standard errors of  $k'$  are the same as those of  $k$  (see equations (2)).

Table 2. Deviations ( $\bar{y}_t - \hat{y}$ ) of the actual values of  $\bar{y}_t$  from those calculated from the regression equations of Table 1

Age (weeks)	G $\times$ S $\delta\delta$	G $\times$ S $\varphi\varphi$	L $\times$ R $\delta\delta$	L $\times$ R $\varphi\varphi$
2	-1	0	+2	+2
3	-1	-2	+1	0
4	+5	+4	0	+1
5	-4	-5	-4	-4
6	-1	-3	-5	-4
7	+2	+4	+1	+2
8	+3	+5	0	+1
9	0	0	+8	+5
10	-4	-4	-3	-3
12	-4	-8	-5	-10
14	-3	-17	-3	-18
17	-18	-36	-22	-34
20	-30	-51	-35	-53
23	-40	-60	-41	-73

All deviations have been multiplied by  $10^3$ .

sets of longitudinal data the use of cross-sectional standard errors could therefore lead to very seriously misleading conclusions.)

The following main points emerge from Tables 1 and 2 and Figs. 1 and 2.

(i) All groups show an approximately linear relationship up to 10 weeks; during this period the average slope,  $k$ , is in all cases substantially greater than the value of  $1/3$ , which would obtain in isometric growth, i.e. shank length is growing more rapidly than the body as a whole. Differences between  $k$  and  $k'$  are negligible.

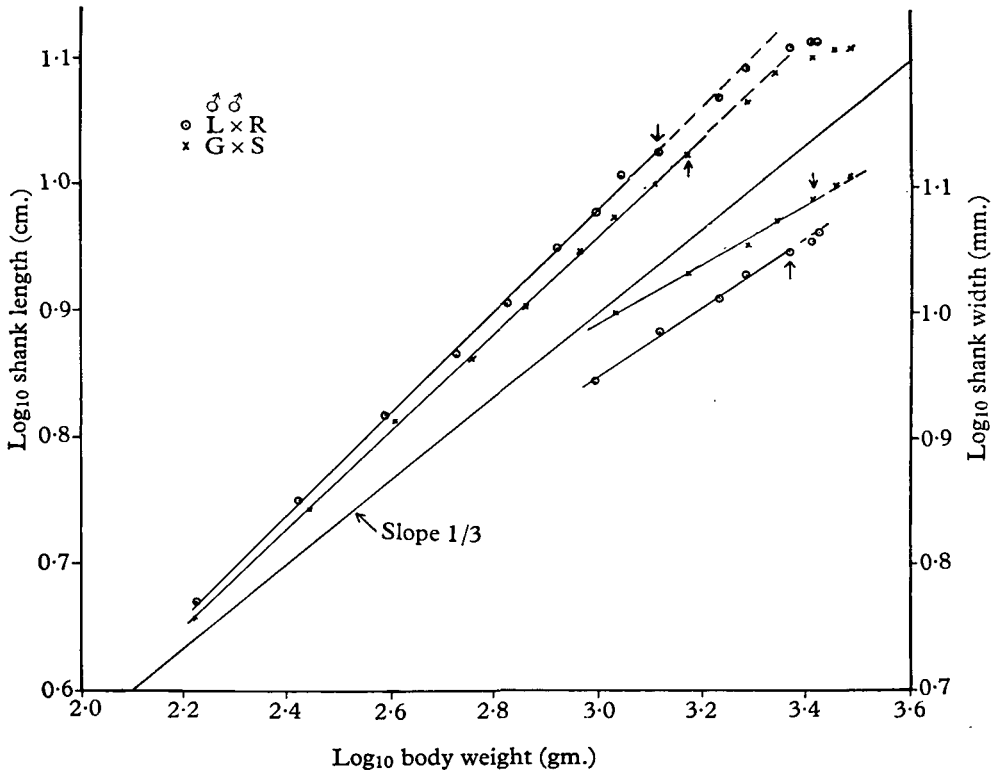


Fig. 1. Group allometry plots up to 23 weeks for males. A line of slope  $1/3$ , representing isometric growth, is drawn in as a guide; the plots above this line are for shank length, those below it for shank width. The regression lines of Table 1 are drawn through the plots, and the last points used in calculating the regression (10 weeks for shank length, 17 weeks for shank width) are indicated by arrows.

(ii) The linear phase is followed by one in which the slope steadily declines until, by about 20 weeks, it is zero; growth in shank length is completed by this age, whereas body-weight is still increasing.

(iii) During the linear phase there is in both sexes a substantial difference in  $k$  between the two crosses of about  $0.019$ ,  $G \times S$  having the lower  $k$ . Differences in  $k$  between the sexes are much smaller; females about  $0.005$  lower in each cross. When the longitudinal standard errors are used, and the results from the two crosses combined, the sex-difference in  $k$  approaches significance at the 5% level.



(iv) The phase of declining slope begins at about 10 weeks in females but not until 14 weeks in males. This is brought out particularly clearly in the sequences of deviations listed in Table 2. In males the 10- and 14-week deviations, although negative, are no larger than many of those which precede them, and the first unequivocal departure from a linear trend occurs at 17 weeks. In females, on the other hand, the non-linear trend is already strongly in evidence at 12 weeks and is quite unmistakable by 14 weeks. There is no question of any abrupt discontinuity in the curves; the division into linear and curvilinear phases is necessarily arbitrary

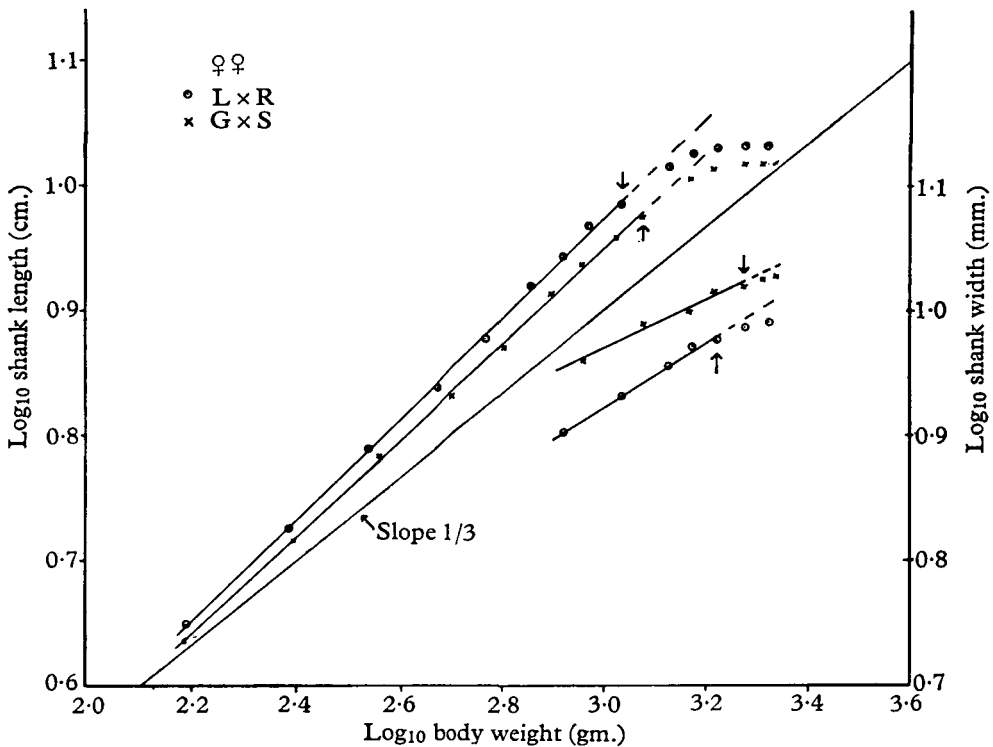


Fig. 2. Group allometry plots up to 23 weeks for females. Explanation as for Fig. 1.

and approximate. But that there is a sex difference of about 4 weeks in this respect is beyond doubt. There also appears to be a sex difference of similar magnitude in the age at which growth in shank length finally ceases.

(v) The deviations from strict linearity up to 10 weeks (Table 2) are small, but not entirely negligible. The largest of them ( $L \times R$   $\text{♂♂}$  at 9 weeks) corresponds to 2 mm., or 2% of the mean value of  $Y$  at that age. Within each cross there is a remarkably close parallelism between the deviations of the two sexes. This indicates (and the subsequent longitudinal analysis will confirm) that the deviations cannot, in the main, be accounted for by factors of a purely random nature. There is little or no parallelism between the deviations of the two crosses, which were kept in adjoining compartments. A more detailed analysis (Cock, 1962) shows that the



deviations are due, in the main, to irregularities in the growth curves (with respect to time) of body-weight, rather than of shank length. Environmental factors of a very local and temporary nature, possibly including sub-clinical outbreaks of disease, seem the most likely causes.

(vi) Throughout the whole of the 2–10-week period, L × R have relatively longer shanks than G × S; by 10 weeks the difference in  $\hat{y}$  amounts to about 0.025 (Table 3).

Table 3. Means and differences, calculated from the equations of Table 1, at body weights corresponding approximately to 2 and 10 weeks of age

	$\hat{y}_{2.2}$ (~ 2 weeks)	$\hat{y}_{3.1}$ (~ 10 weeks)	$\hat{z}_{3.1}$ (~ 10 weeks)
G × S ♂♂	0.6490	0.9997	1.0141
G × S ♀♀	0.6411	0.9868	0.9889
L × R ♂♂	0.6562	1.0227	0.9763
L × R ♀♀	0.6506	1.0136	0.9475
Mean differences:			
♂♂-♀♀	+ 0.0068	+ 0.0111	+ 0.0270
L × R-G × S	+ 0.0084	+ 0.0249	- 0.0396

This is equivalent, in non-logarithmic terms, to a difference of 5.9% in shank length for the same body-weight (or to 15% difference in body-weight for the same shank length). At two weeks the difference is only about one-third as great, the remaining two-thirds being due to the higher  $k$  in L × R. In both crosses males have relatively longer shanks than females; this difference amounts to about 0.011 at 10 weeks (equivalent to 2.6% difference in  $Y$ ), and rather less than half of this has resulted from the higher  $k$  in males over the 2–10-week period.

Growth subsequent to 10 weeks can, again somewhat arbitrarily, be divided into two parts; the phase of declining  $k$  up to 20 weeks, and the subsequent increase in body-weight after growth in shank length has ceased. In the females this division slightly precedes the start of laying; the median age at first egg is roughly 23 weeks. Only approximate comparisons of growth during these periods can be attempted here. The total increments in  $x$  and  $y$  from 10 to 20 weeks are shown for each group in Table 4; the ratio between them will be an estimate of the average  $k$  during this

Table 4. Comparison of growth after 10 weeks

	G × S ♂♂	G × S ♀♀	L × R ♂♂	L × R ♀♀
$\bar{x}_{20} - \bar{x}_{10}$	0.284	0.233	0.295	0.241
$\bar{y}_{20} - \bar{y}_{10}$	0.085	0.042	0.088	0.047
$(\bar{y}_{20} - \bar{y}_{10})/(\bar{x}_{20} - \bar{x}_{10})$	0.299	0.178	0.298	0.193
$\bar{x}_{52} - \bar{x}_{20}$	0.107	0.173	0.096	0.171

period. It is clear that no significance can be attached to the slight differences in the ratios of the two crosses. There is thus no real evidence that the lower  $k$  of G × S up to 10 weeks is reflected in subsequent growth. The main feature of growth beyond

20 weeks is the much greater increase in body-weight in females ( $\bar{x}_{52} - \bar{x}_{20} = 0.172$  in females, 0.102 in males; the two crosses are very similar). This is a reversal of the previous more rapid growth of males, and is undoubtedly due to the tendency for females to lay down large amounts of abdominal fat during and just prior to laying, and to a lesser extent, to the enlargement of the reproductive organs themselves.

(ii) *The shank width: body-weight curves*

Shank width is a less accurate measurement than shank length, and no measurements were taken before 8 weeks, or at 9 weeks; the data have therefore been analysed less fully. The cross-sectional analysis is similar to that carried out for shank length, except that regression lines have been fitted to the 8–17-week period instead of the 2–10-week period. The results are given in Table 1 (b) and the lower plots of Figs. 1 and 2.

At  $x = 3.1$  (see Table 3) G  $\times$  S shanks are 11% thicker but 6% shorter than L  $\times$  R shanks. The sex difference, however, is radically different: male shanks are 6% thicker and 3% longer than female shanks. Thus the sex difference in shank length relative to body-weight is primarily a difference in the relative *size* of the shank as a whole, while the difference between the crosses is primarily a difference in the *shape* of the shank itself.

Little importance can be attached to the group differences in  $k_z$ , and  $k'_z$ , since the appropriate longitudinal standard errors have not been calculated. In all groups  $k_z$  (and  $k'_z$ ) is very much lower than  $k_y$ , but the parameters relate to different age-ranges. Moreover,  $z$  (unlike  $y$ ) appears to be subject to appreciable 'occasion' effects, due to a tendency to press the calipers more firmly together on one day than on another. These could have substantial effects on  $k_z$  estimated over a relatively small increment of  $z$  (but comparisons between groups or individuals would not be affected, since all individuals were measured on the same day). Despite this, it seems clear (at least in males) that  $k_z$  is less than the isometric value of 1/3 at ages when  $k_y$  is still greater than 1/3.

#### 4. LONGITUDINAL ANALYSIS: INDIVIDUAL VARIATION

(i) *The shank length: body-weight relation, 2–10 weeks; differences in relative growth rate ( $k_L$ )*

This analysis is concerned with that part of the  $y$  against  $x$  curve, which, judged by the criteria of section 3, is essentially linear in both sexes, i.e. with the period from 2 to 10 weeks of age. Within this period, longitudinal regression lines have been calculated (one for each individual), in a way exactly analogous to that used in Section 3 for the weekly group means. With a separate straight line fitted to the data of each individual, we can examine more critically the extent to which a series of straight lines is an adequate representation of the data, and discover the extent and significance of individual variation in  $k$ . The initial stages of the analysis may be arranged as an analysis of variance of  $y$ ; the form of the analysis is set out in

Table 5. Model for analysis of variance of  $y$  for longitudinal data

Source of variation	Degrees of freedom	Sum of squares (S.S.)
Joint $k_L$	1	D
Individual variation in $k_L$	$N - 1$	C - D
Positional differences (differences in $\hat{y}_{\bar{x}}$ )	$N - 1$	A + D - B - E
Residual within individuals (total)	$N(n - 2)$	B - C
Non-linearity of the cross-sectional regression	$n - 2$	$N(F - G)$
Interaction: individuals $\times$ non-linearity (error)	$(N - 1)(n - 2)$	$B - C - N(F - G)$
Total	$Nn - 1$	

$N$  individuals are each measured at  $n$  ages. The last two lines involve an approximation (see Text).

A = total S.S. of  $y$  (single measurements) about the overall mean =  $S(y)^2$ .

B = S.S. of  $y$  within individuals =  $\sum_{i=1}^N S_i(y^2)$ .

C = S.S. due to the  $N$  longitudinal regression lines =  $\sum_{i=1}^N \frac{S_i^2(xy)}{S_i(x^2)}$ .

D = S.S. due  $N$  parallel regression lines =  $\frac{\sum_{i=1}^N S_i^2(xy)}{\sum_{i=1}^N S_i(x^2)}$ .

E = S.S. due to one regression line fitted to all the single measurements =  $\frac{S^2(xy)}{S(x^2)}$ .

F = S.S. of the means of  $y$  at each age =  $S_i(y^2)$ .

G = S.S. due to the cross-sectional regression line (fitted to the age-means) =  $\frac{S_i^2(xy)}{S_i(x^2)}$ .

Table 6. Longitudinal analysis of variance of  $y$ , 2-10 weeks

$N$	Degrees of freedom	G $\times$ S ♂♂	G $\times$ S ♀♀	L $\times$ R ♂♂	L $\times$ R ♀♀
		38	27	47	46
Joint $k_L$		0.3893	0.3837	0.4066	0.4029
Joint $k_L$		0.3897	0.3844	0.4074	0.4036
		Mean squares (all $\times 10^{-6}$ )			
(1) Individual variation in $k_L$	$N - 1$	64.6	121.1	103.5	91.1
(2) Positional differences (differences in $\hat{y}_{\bar{x}}$ )	$N - 1$	807.5	520.0	580.9	529.9
(3) Residual: var( $d$ )	$7N$	31.9	38.8	50.7	36.4
(4) Non-linearity of cross-sectional regression	7	405.4	421.3	807.1	498.8
(5) Error (interaction): var $_R(d)$	$7(N - 1)$	21.8	24.1	34.3	26.1

The analysis follows the model of Table 5. For testing lines (1) or (2) against lines (3) or (5), the 0.1% point of F, the variance ratio, is less than 2.4 for G  $\times$  S ♀♀ and less than 2.0 for other groups. For testing line (4) against line (5) the 0.1% point of F is less than 4.0 for all groups. All effects are significant at  $P \ll 0.1\%$  in all groups.

Table 5, and the numerical results are given in Table 6. Table 5 is an extension, making allowance for the different nature of the data, of the method used by Reeve (1940).

Table 6 shows that individual variation in  $k$  is highly significant in all four groups, even when the F test is based (more conservatively) on  $\text{var}(d)$  instead of  $\text{var}_R(d)$ .

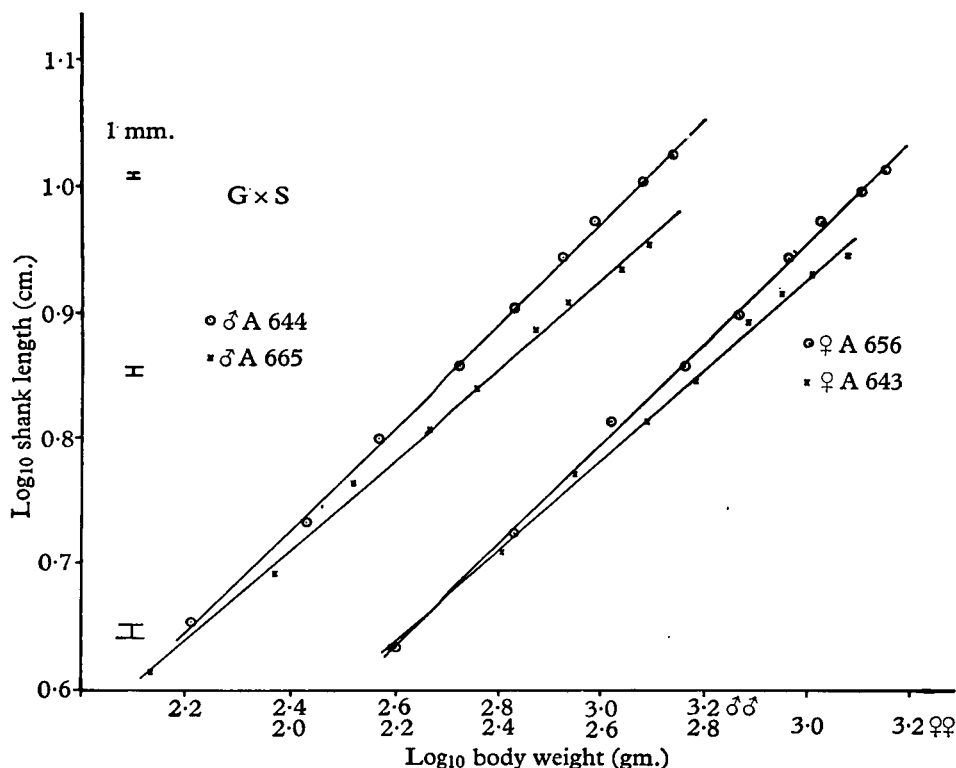


Fig. 3. Selected individual plots ( $G \times S$ ) for shank length: body-weight, 2-10 weeks, with their regression lines. The parameters of the regression lines are given below. The origin of the body-weight scale for females has been shifted to the right to avoid overlapping. These individuals have been chosen to illustrate extremes of individual variation in  $k$ , not because they yield exceptionally close linear fits (compare the values of  $\text{var}(d)$  below with the group means in Table 6). The bars on the left represent 1 mm. at different levels of the logarithmic scale.

	$k_{LW}$	$\hat{y}_x^2$	$\text{var}(d)$ ( $\times 10^{-6}$ )
♂ A 644	0.410	0.888	21.4
♂ A 665	0.360	0.852	49.2
♀ A 656	0.402	0.850	32.6
♀ A 643	0.360	0.830	40.7

The genuineness of differences in  $k_L$  is also clearly apparent on graphical analysis: see Figs. 3 and 4. Positional differences (differences in  $\hat{y}_x^2$ ) are also highly significant, but these have a simple biological interpretation (see Reeve, 1940) only in cases where there is no significant variation in  $k_L$ ; their interpretation in the present data

will be considered in Section 4 (ii). The highly significant mean square due to 'non-linearity of the cross-sectional regression' merely confirms the point already made in section 3 (a), that deviations from linearity are in part systematic, i.e. due to factors common to all members of a group.

The reduced residual variance,  $\text{var}_R(d)$ , measures the magnitude of deviations of single observed values of  $y$  from their respective individual regression lines, after

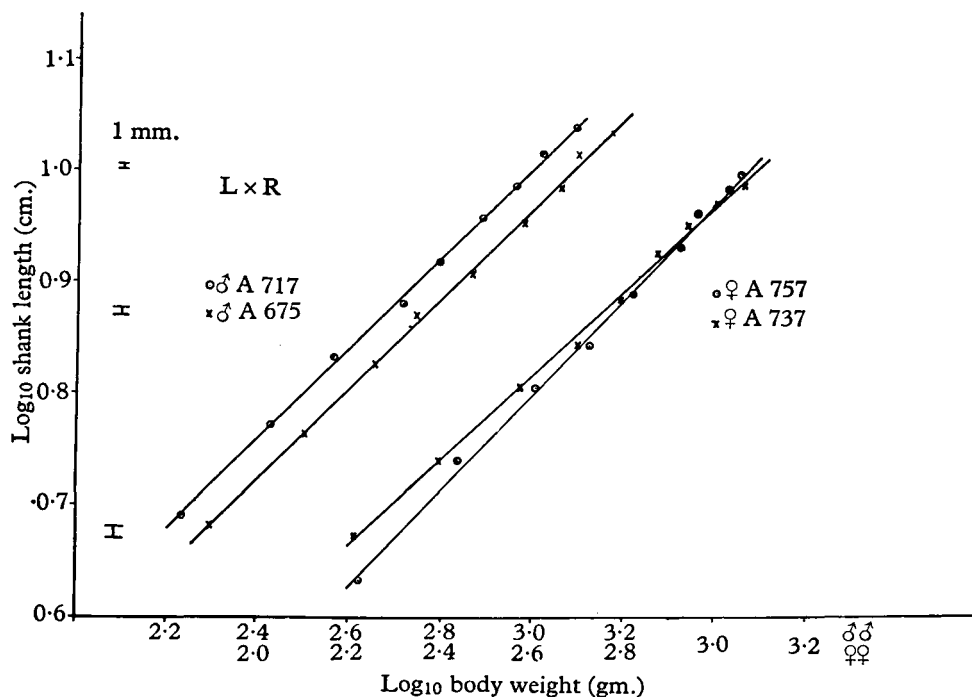


Fig. 4. Selected individual plots ( $L \times R$ ) for shank length: body-weight, 2-10 weeks. Explanation as in Fig. 3. The males have been chosen to show a large difference in  $\hat{y}_z$  with practically identical  $k$ . The females show a large difference in  $k$ , but, in contrast to the two  $G \times S$  pairs of Fig. 3, the lines intersect near the end of the 2-10 week period.

	$k_{LW}$	$\hat{y}_z$	$\text{var}(d)$ ( $\times 10^{-6}$ )
♂ A 717	0.409	0.906	18.0
♂ A 675	0.406	0.870	44.3
♀ A 757	0.433	0.845	52.0
♀ A 737	0.382	0.857	38.4

systematic deviations from linearity have been allowed for. The values of  $\text{var}_R(d)$  for the different groups correspond to a coefficient of error variation in  $Y$  of about 1.2%; in the region of  $\bar{x}$  the standard deviations for error in  $Y$  amount to 0.8 to 1.0 mm. In view of the relatively crude nature of the measurements, these are remarkably low values. They have to cover errors in  $X$  as well as in  $Y$ , and errors of a

biological nature (e.g. for  $X$ , variations in the amount of food and faeces in the alimentary canal at the moment of weighing, and fluctuations in general health and 'condition'), as well as errors of measurement in the narrow sense. Even if the total residual,  $\text{var}(d)$ , is taken as the basis, the coefficient of error variation in  $Y$  rises, in the group ( $L \times R \text{ ♂♂}$ ) with the highest value, only to 1.6%.

At the top of Table 6 are given the 'joint' values of  $k_L$  and  $k'_L$ ; these are weighted means of the individual values of  $k_L$  and  $k'_L$  (each individual value weighted by its own  $S_i(x^2)$ ). They are very nearly identical with each other, and with the cross-sectional values given in Table 1. For future purposes it will be more convenient to use the unweighted means of  $k_L$ ; these (differing only very slightly from the weighted means) are given in Table 7, together with means and variances for the other parameters of the longitudinal regressions.

Table 7. Means and variances of parameters derived from longitudinal analysis

		G × S ♂♂	G × S ♀♀	L × R ♂♂	L × R ♀♀
$k_{L_y}$	mean	0.3897 ± 0.0015	0.3841 ± 0.0025	0.4070 ± 0.0018	0.4034 ± 0.0017
	variance	80.3	164.9	147.3	128.6
	error variance	27.0	33.2	48.3	40.2
$\hat{y}_{\bar{x}}$	mean	0.8807 ± 0.0016	0.8465 ± 0.0015	0.8851 ± 0.0012	0.8549 ± 0.0011
	variance	93.7	58.6	66.2	59.8
	error variance	2.46	2.71	3.86	2.95
$S_i(x^2)$	mean	0.8140 ± 0.0136	0.7358 ± 0.0155	0.7156 ± 0.0100	0.6541 ± 0.0073
	variance	6993	6510	4682	2474
	harmonic mean	0.8058	0.7278	0.7092	0.6502
$S_i(y^2)$	mean	0.1237 ± 0.0020	0.1087 ± 0.0024	0.1188 ± 0.0016	0.1065 ± 0.0014
	variance	152.0	144.9	118.8	87.7
$\bar{x}_i$	mean	2.7946 ± 0.0059	2.7348 ± 0.0059	2.7619 ± 0.0050	2.7065 ± 0.0050
	variance	1324	942	1153	1144
$\bar{y}_i$	mean	0.8807 ± 0.0027	0.8465 ± 0.0028	0.8851 ± 0.0021	0.8549 ± 0.0020
	variance	279	212	217	189
$\hat{z}_{3.1}$	mean	1.0140 ± 0.0027	0.9889 ± 0.0030	0.9762 ± 0.0023	0.9475 ± 0.0023
	variance	285	245	250	253
	error variance	53.4	45.5	68.1	73.6
	(maximum)				

All variances are  $\times 10^{-6}$ . The error variances of  $k_{L_y}$  and  $\hat{y}_{\bar{x}}$  have  $7(N-1)$  and that of  $\hat{z}_{3.1}$  has  $5(N-1) - 2$  degrees of freedom. All other variances have  $N-1$  degrees of freedom.

The error variances of  $k_L$  and  $\hat{y}_{\bar{x}}$  in Table 7 are calculated from the following formulae, which in turn are derived from equations (2) by a process of simple averaging. (The suffix  $H$  denotes the harmonic, instead of the arithmetic mean of  $S_i(x^2)$ ; the harmonic means are given in Table 7.)

$$\left. \begin{aligned} \text{var}_E(k_L) &= \frac{\text{var}_R(d)}{\bar{S}_{H_i}(x^2)}; \\ \text{var}_E(\hat{y}_{\bar{x}}) &= \frac{\text{var}_R(d)}{n} + \bar{S}_i(x^2) \cdot \text{var}_E(k_L) \end{aligned} \right\} \quad (3)$$

These error variances may be compared with the variances of the same parameters in F tests; this naturally gives results almost identical with those obtained in Table 6.

The analysis in this section (and in Section 4 (ii)) is based on the assumption that the basic error variance, estimated by  $\text{var}_R(d)$ , is normally distributed, and that it is (i) homogeneous between individuals, and (ii) uniform over the range of observed values of  $x$ . Individual values of  $\text{var}_R(d)$  have not been computed, but inspection of the individual values of  $\text{var}(d)$  does not reveal any outstandingly aberrant values; the largest within each group are 2 to 3 times the group averages. Assumption (ii) is more dubious; in the case of  $Y$  (but not of  $X$ —see Section 1) equally spaced class intervals (1 mm.), corresponding to decreasing intervals of  $y$ , have been used over the whole range. However, Sheppard's correction ( $c^2/12$ , where  $c$  is the class interval) is small in relation to  $\text{var}_R(d)$  and changes only slowly with age (about  $8 \times 10^{-6}$  at 2 weeks, and  $2 \times 10^{-6}$  at 10 weeks). It is also true that actual errors of measurement (including biological errors due to disturbances of growth) are likely to be higher on a logarithmic scale at the younger ages. Nevertheless, it seems very unlikely that departures from strict veracity in assumptions (i) or (ii) could have an appreciable effect on any of the conclusions drawn, particularly in view of the fact that all comparisons are significant well beyond the 0.1% probability level.

A further assumption (or, rather, approximation) is involved in equation (3) and in the partition in Tables 5 and 6 of  $\text{var}(d)$  into  $\text{var}_R(d)$  and a component due to non-linearity of the cross-sectional regression. These would be exact if  $x$  were a true independent variable, and each individual had been measured at the same series of values of  $x$ , instead of at the same series of ages. In the present instance variation in  $x$ , and in increments in  $x$ , between individuals is small in relation to variation between ages in the same individual: from Table 7,  $S_i(x^2)$  is about 600 times as great as  $\text{var}(\bar{x}_i)$  and 100 to 300 times as great as  $\text{var}(S_i(x^2))$ . The difference between  $\text{var}(d)$  and  $\text{var}_R(d)$  is also fairly small (Table 6). The probable effect of these approximations therefore seems to be trivially small.

(ii) *The relation between differences in  $\hat{y}$  and  $k_y$*

It has been shown that, within each group, there is significant individual variation in  $k$ . This implies that the variance of  $\hat{y}$  will change systematically according to the value of  $x$  at which it is measured. The value  $\bar{x}$ , is statistically important in that it minimizes the average error variance of  $\hat{y}$ , but it has no particular biological importance, since it is determined by the arbitrary series of ages at which measurements are taken. Since differences in  $k$  will automatically produce differences in  $\hat{y}$ , the important question is whether *all* the differences in  $\hat{y}$  can be regarded as the result of differences in  $k$ . If this were the case, we should expect the lines for different individuals all to intersect (within the limits of error) at a common point. Further, if a high or low  $k$  were something characterizing the whole period of growth of the shank, we should expect the point of intersection (concurrence) to



occur during early embryonic development: at or soon after the time when the limb bones are first formed.

This needs some qualification in view of the fact that  $k_y$  itself is considerably higher during embryonic life than during post-natal growth (Landauer, 1934; Lerner, 1936). The hypothesis can be reformulated to take such changes into account. Thus it might be assumed that during each phase of growth a pair of individuals are characterized by a difference in  $k$  which remains constant from phase to phase. Alternatively, the ratio between the  $k$ -values could be assumed to remain constant for each phase. On the first form of the hypothesis (constant difference in  $k$ ) the point of concurrence would give the 'initial' value of  $x$ ; on the second form (constant ratio) it would give the 'initial' value of  $y$ . In either case it is necessary to assume that changes in  $k$  (whether abrupt or gradual) occur at the same value of  $x$  in all individuals, rather than at the same age. This is unlikely to be strictly true, but it is an integral part of any hypothesis that differences in  $k$  are the sole cause of differences in  $\hat{y}$ . Clearly, no exact 'initial' values for  $x$  or  $y$  can be formulated in connection with the hypothesis; growth of the shank cannot be said to begin at any precise stage of development. All that the hypothesis demands is that the point of concurrence should represent an initial value reasonably early in development. As an approximate yardstick we may take  $x = 0$  ( $X = 1$  g.) and  $y = -0.7$  ( $Y = 0.2$  cm.), which, in Landauer's (1934) data, fall between the 7th and 8th day of incubation.

It is evident from graphical analysis that the lines within each group are not in fact concurrent, nor sufficiently nearly concurrent to be compatible with the extent of errors of measurement. The two pairs of lines shown in Fig. 3 both intersect near 2 weeks of age, but one pair in Fig. 4 intersects near 8 weeks, and the other pair are practically parallel, i.e. do not intersect at all. (Although the four pairs illustrated come one from each group, a similar range of conditions can be found within any one group.) For a more quantitative test of the hypothesis we need to discover, for a set of regression lines, (i) a significance test for concurrence, and (ii) the location of the point of concurrence, if it exists. An approximate method for this has been developed; the derivation and limitations of the method are given in the Appendix. The numerical results of applying it to the present data are given in Table 8.

The method consists essentially in finding the value of  $x$  at which the variance of the intercepts ( $\hat{y}_a$ ) of the regression lines with a line parallel to the  $y$ -axis is minimized. Since  $\text{var}_E(\hat{y}_a)$  increases as we move away from  $\bar{x}_i$  (see equations (2)), minimizing  $\text{var}(\hat{y}_a)$  would give a biased result; the 'true variance' of  $\hat{y}_a$  ( $\text{var}_T(\hat{y}_a)$ , defined as  $\text{var}(\hat{y}_a) - \text{var}_E(\hat{y}_a)$ ) is therefore minimized instead. The minimum point is taken as giving the nearest approach to the condition that the lines pass through a common point, and satisfaction of this condition (i.e. the hypothesis that  $\text{var}_T(\hat{y}_a)$  is not significantly different from zero) is tested by an F test comparing  $\text{var}(\hat{y}_a)$  and  $\text{var}_E(\hat{y}_a)$ .

The results shown in Table 8 are decisively against the hypothesis that all the individual variation within groups is 'due to' variation in  $k$ . In all four groups the lines are highly significantly non-concurrent, and the point of nearest concurrence occurs, not at an early embryonic stage, but at an age which (in three of the four

groups) is actually within the 2–10-week period to which the measurements relate. On the other hand, variation in  $k$  is responsible for a substantial fraction of the variation in  $\hat{y}$ , as is shown by the estimates at the foot of Table 8 of  $\text{var}_T(\hat{y})$  at values of  $x$  corresponding approximately to 2 and 10 weeks of age. In three of the groups  $\text{var}_T(\hat{y})$  is roughly doubled between 2 and 10 weeks; in the fourth group ( $L \times R \text{ } \text{♀♀}$ , with an unusually late point of nearest concurrence) the fall in  $\text{var}_T(\hat{y})$  between 2 weeks and the minimum almost exactly cancels out the subsequent rise up to 10 weeks.

Table 8. *Test for concurrence of longitudinal regression lines (y on x, 2–10 weeks)*

	G × S ♂♂	G × S ♀♀	L × R ♂♂	L × R ♀♀
At minimum of $\text{var}_T(\hat{y}_a)$ :				
$x = \bar{x} + a =$	1.979	2.470	2.366	2.627
Corresponding mean age (weeks):	1.2	3.5	2.7	4.6
$\text{Var}(\hat{y}_a) =$	76.3	51.6	58.3	59.5
$\text{Var}_E(\hat{y}_a) =$	20.4	5.0	11.4	3.2
$F = \text{var}(\hat{y}_a)/\text{var}_E(\hat{y}_a) =$	3.7	10.2	5.1	18.6
$\text{Var}_T(\hat{y}_a) =$	55.9	46.6	46.8	56.3
$\text{Var}_T(\hat{y}_{2.2}) (\simeq 2 \text{ weeks}) =$	58.6	56.2	49.6	72.4
$\text{Var}_T(\hat{y}_{3.1}) (\simeq 10 \text{ weeks}) =$	122.9	99.0	100.3	76.1

All variances are  $\times 10^{-6}$ . The 0.1% point of F, with  $N - 2$  and 7 ( $N - 1$ ) degrees of freedom, is less than 2.4 for G × S ♀♀ and less than 2.0 for other groups; all groups are therefore non-concurrent at  $P < 0.1\%$ .

No attempt has been made to set confidence limits to the points of nearest concurrence; it is clear from the smallness of the changes in  $\text{var}_T(\hat{y})$  between 2 weeks and the minimum (particularly in the two groups of males) that the minimum points are estimated only within fairly wide margins of error. It seems likely that the differing estimates of the minimum points for the four groups could all represent chance deviations from a common mean; the fact that the coefficients of correlation between  $k$  and  $\hat{y}_x$  are not significantly heterogenous in the four groups (see Table 9) lends *prima facie* support to this view.

The F tests in Table 8 are more sensitive than those carried out in Section 4 (i) to departures from the assumption that the error variance of  $y$  is uniform over the range of  $x$ . Even if we make generous allowance for this by doubling the estimates of  $\text{var}_E(\hat{y}_a)$  at the minimum (which in effect assumes that  $\text{var}_R(d)$  increases by a factor of considerably more than 2 between 2 and 10 weeks) the F test still yields highly significant values. Nevertheless, there is almost certainly some upward bias due to this cause in the estimates of the points of minimum  $\text{var}_T(\hat{y}_a)$ , though not enough to make the true minima fall into embryonic life.

The same hypothesis in relation to differences between groups can be tested (to a sufficient approximation for present purposes) by finding the points of intersection of the cross-sectional regression lines (Table 1). The lines for G × S and L × R

intersect at  $x = 1.75$  in the males and  $x = 1.65$  in the females, i.e. in both sexes at  $X$  about 50 g., which occurs a few days after hatching. These results again do not support an assumed point of concurrence early in embryonic life.

(iii) *The shank width: body-weight relation, 8–17 weeks; positional differences*

In view of the limitations on the scope and accuracy of the data, it has not been thought worth while to carry out a complete longitudinal analysis for shank width. It seemed unlikely that such an analysis would in fact yield any strong evidence of significant individual variation in  $k$ , and a negative result in this respect would merely reflect the imprecision of the data.

Only a partial and approximate analysis has therefore been carried out. For each individual, the value of  $\bar{z}_i$  (for the 8–17-week period) has been corrected to give  $\hat{z}_{3.1}$ , using the values of  $k_C$  given in Table 1. Group means and variances of the individual values of  $\hat{z}_{3.1}$ , calculated in this way, are given in Table 7. A maximum estimate of the basic error variance ( $\text{var}_R(d_z)$ ) has been obtained by deducting from the sum of squares within ages  $\left[ \sum_{t=8}^{17} S_t(z^2) \right]$  the sum of squares attributable to variation in  $z$ , i.e.  $n \cdot \text{var}(\hat{z}_{3.1})$ , where  $n = 5$ . (In taking the sum of squares within ages we are in effect deducting from the total sum of squares of  $z$  the portions attributable to  $k$ , and to systematic age deviations from linearity, on the assumption that all individuals have the same series of values of  $x$ , as well as the same  $k$ . The corresponding deductions allowing for individual variation in  $x$  will always be greater than this.) The corresponding maximum estimates of  $\text{var}_E(\hat{z}_{3.1})$ , derived in accordance with equations (2), are given in Table 7. Even on this conservative basis the significance of individual variation in  $\hat{z}$  is beyond question; the variances of  $\hat{z}$  are 3 to 5 times their respective error variances (the 0.1% point of  $F$  is about 2.0). Deducting  $\text{var}_E(\hat{z}_{3.1})$  from  $\text{var}(\hat{z}_{3.1})$  yields estimates of the true variance ( $\text{var}_T(\hat{z}_{3.1})$ ) of about  $200 \times 10^{-6}$ , i.e. about twice as high as the estimates of  $\text{var}_T(\hat{y}_{3.1})$  (Table 8). Thus, even when the lower precision of measurement and estimation is allowed for,  $\hat{z}$  is an inherently more variable character than  $\hat{y}$ , at least in the age-range around 10 weeks. This greater variability of  $\hat{z}$  is also reflected in the magnitude of differences between groups (see Table 3).

## 5. STATIC ANALYSIS

The coefficients of static allometry at 10 weeks of age have been calculated. The values for the four groups do not differ significantly, and the pooled values (based on within-group variation only; 153 degrees of freedom) are:  $k_{Sy10} = 0.344 \pm 0.22$ ,  $k'_{Sy10} = 0.440$ ;  $k_{Sz10}^5 = 0.419 \pm 0.034$ ,  $k'_{Sz10} = 0.591$ . Note that, despite the pooling of results,  $k_S$  (or  $k'_S$ ) is far less accurately determinable than  $k_o$ ; the standard error of  $k_{Sy}$  is higher, by a factor of about 10, than those of the group means of  $k_{Ly}$  (Table 7). For the first time, too, corresponding values of  $k$  and  $k'$  differ materially, and the problem of deciding between them becomes important. No theoretically

'best' estimate of the coefficient of allometry is in fact possible, except on the basis of *a priori* assumptions about the relative magnitudes of the error variances of  $x$  and  $y$  (or of  $x$  and  $z$ );  $k'$  is the 'best' estimate on the assumption that these form equal fractions of the respective total variances (Teissier, 1948; Kermack & Haldane, 1950). This is clearly a more realistic assumption than that underlying  $k$  (that the error variance of  $x$  is zero). In any case, it is clear (whether we take  $k$ ,  $k'$ , or some other estimate) that the coefficient of static allometry for  $y$  (at least at 10 weeks) does not differ greatly from the ontogenetic coefficient, whereas for  $z$  the static coefficient is much higher than the ontogenetic coefficient (which is about 0.20 to 0.25; Table 1).

Coefficients of static allometry measured at different ages will not in general be equal. The regression of  $\bar{y}_i$  on  $\bar{z}_i$  may be regarded as yielding a kind of 'average coefficient of static allometry over the whole 2-10-week period. This gives (again pooling results from the four groups)  $k_{SY} = 0.369 \pm 0.019$ ,  $k'_{SY} = 0.439$ , which do not differ materially from the 10-week values.

6. SIZE, GROWTH RATE AND SHAPE

The parameters  $\hat{y}_{\bar{z}}$  and  $\hat{z}_{3.1}$  are each measures of simple aspects of shape; they are estimates of the (logarithmic) shank length and width measured at a fixed body-weight. The parameter  $k_{LY}$  (or, more strictly,  $k_{LY} - 1/3$ ;  $1/3$  being the value corresponding to constant shape) measures rate of change of shape (with respect to  $x$ ). In Section 4 we were concerned with individual variation in size (at a given age), and in rate of growth with respect to time, only indirectly, in so far as the effects of such variation had to be eliminated in determining the parameters  $k_{LY}$ ,  $\hat{y}_{\bar{z}}$  and  $\hat{z}_{3.1}$ . There might, however, be reasons of a genetic or physiological nature why particularly large or rapidly growing individuals should have values of  $k_{LY}$ ,  $\hat{y}_{\bar{z}}$  or  $\hat{z}_{3.1}$  above (or below) the average. Possibilities of this nature have been examined by calculating the matrix of correlations between the seven parameters of Table 7. The results (pooled within groups) are given in Table 9.

Table 9. Correlations (pooled within groups) between the seven parameters of Table 7

		Shape		Size		Growth rate	
		$\hat{y}_{\bar{z}}$	$\hat{z}_{3.1}$	$\bar{x}_i$	$\bar{y}_i$	$S_i(x^2)$	$S_i(y^2)$
Rate of change of shape	$k_{LY}$	+0.326	-0.020	+0.167	+0.321	-0.274	+0.323
Shape	$\left\{ \begin{array}{l} \hat{y}_{\bar{z}} \\ \hat{z}_{3.1} \end{array} \right.$		-0.116	-0.111	+0.444	-0.172	+0.017
				+0.357	+0.266	-0.131	-0.134
Size	$\left\{ \begin{array}{l} \bar{x}_i \\ \bar{y}_i \end{array} \right.$				+0.841	+0.096	+0.190
						-0.035	+0.187
Growth rate	$S_i(x^2)$						+0.818

Each value in the table is the mean of the correlation coefficients for the four groups, weighted according to Fisher's z-transformation. (No set of coefficients for the same pair of parameters is significantly heterogeneous, and the total heterogeneity  $\chi^2$ , with 63 degrees of freedom, is 61.8). Significance levels for differences from zero are: 0.159 ( $P = 5\%$ ), 0.208 ( $P = 1\%$ ), 0.259 ( $P = 0.1\%$ ).

The choice of this particular set of parameters was partly a matter of convenience. It is in any case evident from the preceding analysis (particularly Section 4 (ii)), that any interrelationships between size, growth rate and shape parameters will change with the age at which they are measured. Short of the impracticable task of disentangling this changing network of relations fully, the best that can be done is to examine the relations between a set of somewhat arbitrarily chosen parameters. The parameters  $\bar{x}_i$  and  $\bar{y}_i$  may each be regarded as measures of size ('average' size over the whole 2–10-week period). Less obviously,  $S_i(x^2)$  and  $S_i(y^2)$  (or, rather, their square roots) are closely related to the average growth rates of  $x$  and  $y$  with respect to time. This is clearer if we consider that  $k'_{Ly}$ , which estimates the ratio between the growth rates of  $y$  and  $x$ , is equal to  $[S_i(x^2)/S_i(y^2)]^{1/2}$ . (Since the variances of  $S_i(x^2)$  and  $S_i(y^2)$  are small in relation to their means (Table 7), a square-root transformation would have only a slight effect on the correlations.)

Two of the correlations in Table 9 stand out as far higher than any others; those between the two size parameters and between the two growth rate parameters. With each of these pairs the proportion of associated variation (measured by  $r^2$ ) is over 66%. Thus individual variation in size is predominantly variation in *general* size (affecting  $x$  and  $y$  together); variation in shape ( $\hat{y}_{\bar{x}}$ ), important and highly significant though it is, makes a much smaller contribution to the total variation. Similarly, variation in growth rate is predominantly variation in *general* growth rate, and variation in *relative* growth rate ( $k_{Ly}$ ) makes a relatively small contribution.

Many of the remaining correlations are not significantly different from zero, and  $r^2$  is always less than 20%, and usually less than 3%. Besides, some of these correlations are partly spurious, because of algebraic relations between the various parameters. Spurious correlations (in the directions actually found) are to be expected between  $\hat{y}_{\bar{x}}$  and the two size parameters, and  $k$  and the two growth-rate parameters. The biological interpretation of the correlation between  $k$  and  $\hat{y}_{\bar{x}}$  has been dealt with elsewhere (Section 4 (ii) and Appendix), but this correlation does introduce a spurious element into the correlations between  $k$  and the size parameters, and  $\hat{y}_{\bar{x}}$  and the growth rate parameters, which may be removed by calculating partial correlations. After discounting spurious correlations, the following points of interest remain.

(i) There is a positive correlation between size and  $k_y$ . The partial correlations of  $k_y$  with  $\bar{x}$  and  $\bar{y}$  (variation in  $\hat{y}_{\bar{x}}$  eliminated) are +0.216 and +0.208 ( $P \approx 1\%$ ). A similar tendency is apparent in the simple correlations of  $S(y^2)$  with  $\bar{x}$  and  $\bar{y}$ , which are both significantly positive, whereas those of  $S(x^2)$  with  $\bar{x}$  and  $\bar{y}$  are insignificant. It thus appears that the larger individuals tend to have an increased growth rate in shank length unaccompanied by a corresponding increase in the growth rate in body-weight; hence the higher  $k_y$ . This effect, however, is a very small one, and differences between the two crosses (see Section 3) show a reversal of this tendency; G  $\times$  S are larger than L  $\times$  R, but have a lower  $k_y$ .

(ii) Both size parameters have highly significant positive correlations with  $\hat{z}_{3.1}$ . (Spurious contributions to these correlations can hardly be important, since the age-range from which  $\hat{z}_{3.1}$  is estimated only partially overlaps that used for the other



parameters). In this case the differences between groups (between sexes as well as between crosses) agree with the within-group variation in showing a tendency for large size to be associated with a higher relative shank width. The fact that  $k_{sz}$  is much greater than  $k_{oz}$  (Section 5) is another expression of the same phenomenon. (It may be shown algebraically (see Teissier, 1948) that, given an exact fit to ontogenetic allometry, and the same  $k_0$  in all individuals, a zero correlation between  $y$  and  $x$  implies  $k'_s = k'_o$ , and a positive correlation implies  $k'_s > k'_o$ .)

(iii) The correlation between  $\hat{y}_{\bar{x}}$  and  $\hat{z}_{3.1}$  is negligibly small. (It would be more logical to measure  $\hat{z}$  and  $\hat{y}$  at the same value of  $x$ ; the correlation between  $\hat{y}_{3.1}$  and  $\hat{z}_{3.1}$  differs only slightly from that between  $\hat{y}_{\bar{x}}$  and  $\hat{z}_{3.1}$ :  $-0.085$  as against  $-0.116$ ). The error variances of these two parameters are too low (see Table 7) for errors of estimate alone to account for the absence of any appreciable correlation between them. It seems rather that the within-group variation in  $\hat{y}$  is a compound of two anatomically different types, in approximately equal amounts. One type (like the difference between the sexes—see Section 3 (ii)) represents variation in the relative *size* of the shank as a whole, and changes  $\hat{y}$  and  $\hat{z}$  in the same direction. The other type (like the difference between  $G \times S$  and  $L \times R$ ) represents variation in the *shape* of the shank itself, and changes  $\hat{y}$  and  $\hat{z}$  in opposite directions.

## 7. DISCUSSION

Before discussing the findings on the general shape of the allometry curves, it is desirable to mention that the main findings have been confirmed, and in some respects extended, by measurements made in the course of the selection experiments. The allometry coefficients for shank width ( $k_{Cz}$ ), 2–10 weeks, vary in different hatches, but are always substantially lower than those for shank length ( $k_{Cy}$ ) (average 0.31, as against 0.4). The existence of a sex difference (males higher) in  $k_{Cy}$  and  $k_{Cz}$  has been confirmed.

The occurrence of a decline in  $k_{Cy}$ , the onset of which is earlier in females than in males, is in agreement with the results of Jaap (1943) although in his material, and in that of Gilbreath & Upp (1952), the decline is even further delayed; this could be ascribed to different genetic material, or to different nutritional and husbandry régimes, but it seems likely that the latter is the major cause. The sex difference in relative shank length consists, ontogenetically, of two distinct parts; (i) a small part which develops gradually up to 10 weeks, due to the higher  $k_y$  in males, and (ii) a much larger part which develops rather suddenly between 10 and 14 weeks, due to the delayed decline in  $k_y$  in males. The timing of this second part suggests that it is dependent on the sex hormones (c.f. Tanner (1962) for some sexual differences in human conformation which develop during or just prior to puberty).

Longitudinal analyses of various measurements in terms of linear allometry have been reported by Kidwell and others for cattle (Kidwell, Gregory & Guilbert, 1952) and for fowls (Kidwell & Williams, 1956). No residual variances ( $\text{var}(d)$  or  $\text{var}_R(d)$ ) are given, however, so that the significance of individual differences cannot be assessed. Their analyses of positional differences are vitiated by the use of  $\hat{y}_0$  (i.e.

the intercept with the  $y$ -axis); the distant extrapolation introduces large errors of estimate and a spurious negative correlation with estimates of  $k$ . Moreover the age means given for the fowl data show that most of the relations are strongly curvilinear.

The present longitudinal analysis shows that individual variation in shank length at a given body-weight is complex in its ontogenetic origin. Variation in post-natal (2–10 weeks)  $k_y$  is an important cause of such variation, but not the only cause. The nature of the other cause or causes can be discovered only by a study of embryonic and early post-natal growth. They may include variation in embryonic  $k_y$  which is unrelated to post-natal  $k_y$ , and variation in the body-weight at which the transition between different 'phases' of growth (with different values of  $k_y$ ) occurs. Variation in relative shank length is also complex anatomically, and is of at least two kinds (two being the maximum demonstrable with a set of only three measurements); that due to variation in the shape of the shank itself, and that due to variation in the relative size of the shank as a whole. These ontogenetic and anatomical complexities have been demonstrated primarily at the phenotypic level of variation, but they also occur at the genetic level, in differences between the sexes and crosses. Although some minor differences in the growth curves of  $G \times S$  and  $L \times R$  (see Section 3 (i), point (v)) may be due to their having been reared separately, there is little doubt that the major differences are of genetic, not environmental origin.

#### 8. SUMMARY

Body-weight and shank length from 2 weeks of age to adult (and from 8 weeks onwards, shank width) have been measured on 154 fowls all hatched on the same date, belonging to two  $F_1$  breed crosses: White Leghorn  $\times$  Rhode Island Red ( $L \times R$ ) and Indian Game  $\times$  Light Sussex ( $G \times S$ ). After logarithmic transformation the data have first been analysed cross-sectionally (analysis of the age-means for each sex and cross). A longitudinal analysis (fitting a regression line to the data of each individual) has then been made of the approximately linear portions of the curves. The following conclusions are drawn.

(1) Growth in shank length relative to body-weight between 2 and 10 weeks conforms closely to simple allometry. The coefficient of ontogenetic allometry (heterauxesis),  $k$ , is approximately 0.4, being 0.02 higher in  $L \times R$  than in  $G \times S$  and 0.05 higher in males than in females. In females  $k$  declines (eventually to zero) after 10 weeks; the decline occurs about 4 weeks later in males. For shank width relative to body-weight  $k$  is about 0.25.

(2) At a given body-weight males have longer and thicker shanks than females;  $L \times R$  have longer but thinner shanks than  $G \times S$ .

(3) Within sexes and crosses there is highly significant individual variation in  $k$ , but the allometry lines do not pass, within the limits of error, through any single point. This implies that variation in relative shank length is complex in its ontogenetic origin.



(4) There is no appreciable correlation within sexes and crosses between shank width and shank length at a given body-weight; this implies (as does (2)) that variation is also complex anatomically.

(5) Differences in shape and rate-of-change of shape contribute only a small part of the total variation within sexes and crosses; most is due to differences in *general* size and *general* growth rate.

(6) Shank width at a given body-weight is positively correlated with body-weight at a given age ( $r = +0.36$  within sexes and crosses). This agrees with the finding that the coefficient of static allometry (allomorphosis) for shank width is much higher than the ontogenetic coefficient. For shank length the ontogenetic and static coefficients are approximately the same.

I am greatly indebted to Dr E. C. R. Reeve and Mr G. J. S. Ross for their criticisms; to Mr Ross also for providing the reference to Williams's test for concurrence and the worked example comparing Williams's test with that given in the Appendix.

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APPENDIX

*An approximate significance test for concurrence of regression lines*

The following test was developed in ignorance of that proposed by Williams (1953). Williams constrains the lines to pass through a general point, and then minimizes the sum of squares of deviations of observations from the constrained lines. This approach is the reverse of that used here, which is to minimize the sum of squares of deviations of the lines from the general point. The computations are much less heavy than those involved in Williams's method, and the present method appears to give a good approximation, at least when the number of regression lines is large and the deviations from linear regression are small.

Using the notation of the body of the paper, since

$$\hat{y}_a = \hat{y}_{\bar{x}} + ak$$

$$\left. \begin{aligned} \text{var}(\hat{y}_a) &= \text{var}(\hat{y}_{\bar{x}}) - 2a \cdot \text{cov}(\hat{y}_{\bar{x}} k) + a^2 \text{var}(k) \\ \text{cov}(\hat{y}_a k) &= \text{cov}(\hat{y}_{\bar{x}} k) + a \cdot \text{var}(k) \end{aligned} \right\} \quad (4)$$

The minimum value of  $\text{var}(\hat{y}_a)$  will occur when

$$\left. \begin{aligned} a &= \frac{-\text{cov}(\hat{y}_{\bar{x}} k)}{\text{var}(k)} \\ \text{and, at this value of } a, \quad \text{cov}(\hat{y}_a k) &= 0 \\ \text{and} \quad \text{var}(\hat{y}_a) &= \text{var}(\hat{y}_{\bar{x}}) \cdot (1 - r^2) \end{aligned} \right\} \quad (5)$$

where  $r$  is the coefficient of correlation between  $\hat{y}_{\bar{x}}$  and  $k$ . (Equations (4) and (5) are valid, *mutatis mutandis*, for any two values of  $x$  separated by a distance  $a$ , but the use of  $\bar{x}$  is essential to the formulae to be given below.)

Minimizing  $\text{var}(\hat{y}_a)$  may be regarded as finding the closest approach to the condition that the values of  $\hat{y}_a$  for all the lines are identical, i.e. that the lines are concurrent. But since the error variance of  $\hat{y}_a$  ( $\text{var}_{\text{E}}(\hat{y}_a)$ ) increases as we move away from  $\bar{x}$  (see equations (2)), the estimate of the point of nearest concurrence derived from equation (5) will be biased towards  $\bar{x}$ . This bias may be removed (or almost removed) by minimizing the 'true' variance of  $(\hat{y}_a)$ , defined as  $\text{var}_{\text{T}}(\hat{y}_a) = \text{var}(\hat{y}_a) - \text{var}_{\text{E}}(\hat{y}_a)$ . Formulae for  $\text{var}_{\text{E}}(\hat{y}_{\bar{x}})$  and  $\text{var}_{\text{E}}(k)$  are given in equations (3) (in the body of the paper); together with equations (2) and (4), these yield:

$$\left. \begin{aligned} \text{var}_{\text{E}}(\hat{y}_a) &= \text{var}_{\text{E}}(\hat{y}_{\bar{x}}) + a^2 \text{var}_{\text{E}}(k) \\ \text{var}_{\text{T}}(\hat{y}_a) &= \text{var}_{\text{T}}(\hat{y}_{\bar{x}}) + a^2 \text{var}_{\text{T}}(k) \end{aligned} \right\} \quad (6)$$

The minimum of  $\text{var}_{\text{T}}(\hat{y}_a)$  will occur when

$$\left. \begin{aligned} a &= \frac{-\text{cov}(\hat{y}_{\bar{x}} k)}{\text{var}_{\text{T}}(k)} \\ \text{and is equal to } \text{var}_{\text{T}}(\hat{y}_{\bar{x}}) (1 - r_*^2), \text{ where} \\ r_*^2 &= \frac{\text{cov}^2(\hat{y}_{\bar{x}} k)}{\text{var}_{\text{T}}(\hat{y}_{\bar{x}}) \text{var}_{\text{T}}(k)} \end{aligned} \right\} \quad (7)$$

The expression  $r_*$  may be regarded as a modified coefficient of correlation between  $\hat{y}_{\bar{x}}$  and  $k$ ; a coefficient corrected for 'attenuation' (Kelley, 1947). The value of  $x$  at the estimated point of nearest concurrence is given by  $\bar{x} + a$ , and the value of  $y$  may be found from this and the joint regression line.

The significance test consists in comparing  $\text{var}(\hat{y}_a)$  with  $\text{var}_E(\hat{y}_a)$  in an ordinary F test, as has been done in Table 8. A significant value of F indicates that the lines are non-concurrent. (All the figures needed for calculating Table 8 are given in Tables 6 and 7, except for the values of  $\text{cov}(\hat{y}_{\bar{x}}k)$ . These are +43.4, +34.9, +39.2 and +7.0 (all  $\times 10^{-6}$ ) for  $G \times S \text{ ♂♂}$ ,  $G \times S \text{ ♀♀}$ ,  $L \times R \text{ ♂♂}$  and  $L \times R \text{ ♀♀}$  respectively.)

In general,  $\text{var}(\hat{y}_a)$  will have  $N - 1$  degrees of freedom, but in estimating the point of nearest convergence one degree of freedom will be lost. This is clear if the case of  $N = 2$  is considered; unless the lines are exactly parallel (which have an infinitesimal probability of occurrence) there will always be a value of  $a$  for which  $\text{var}(\hat{y}_a)$  is zero. For the purposes of carrying out the F test for concurrence, therefore,  $\text{var}(\hat{y}_a)$  should be derived by dividing the relevant sums of squares and cross-products by  $N - 2$ , but for estimating  $\text{var}_T(\hat{y}_a)$  at a previously specified value of  $a$  (e.g. for comparing different values of  $a$ ), the divisor  $N - 1$  should be used. (In Table 8,  $N - 1$  has been used throughout; the effect is to give values of F slightly lower than the correct ones.)

The sensitivity of the test (i.e. the likelihood of obtaining strong evidence against concurrence) will, other things being equal, be less when the point of nearest concurrence is far distant from  $\bar{x}$  (i.e.  $a$  is large), since  $\text{var}_E(\hat{y}_a)$  will then be large. In addition, if  $a$  is so large that the point falls outside the range of measured values of  $x$ , the underlying assumptions of linearity of regression and uniformity of residual variance, over the whole range of  $x$ , will be more dubious. (Points of concurrence outside the range of linearity may, in certain circumstances, be given a meaning—see Section 4 (ii).) Certain other assumptions are involved in the test.

(i) It is assumed that  $x$  is measured without error.

(ii) Once the point of nearest concurrence has been found, the values of  $k$  and  $\hat{y}_a$  will need adjustment to provide the best fit to this point together with the observed values of  $x$  and  $y$  for each line. It is assumed that the effect of these adjustments will be negligible when the original fit to linear regression is good and the point is not far outside the range of observed values.

(iii) Equations (8) will only be strictly valid where each line has the same value of  $\bar{x}_i$ . The right hand sides will otherwise include a term due to the covariance of  $\text{var}_E(\hat{y}_{\bar{x}})$  and  $\text{var}_E(k)$ , but this term will be negligibly small if variation in  $\bar{x}_i$  and  $S_i(x^2)$  is small or uncorrelated.

For reasons given in Section (4) (for (iii) see also Table 9) the effect of departures from these assumptions on the outcome of the tests in Table 8 appear to be very slight.

A simple example comparing the present test with that of Williams has been calculated, using four regression lines, with  $x = 2, 3, 4, 5, 6$  for all lines, and  $y = 3, 5, 8, 10, 13; 2, 4, 5, 7, 9; 1, 2, 3, 5, 7; 2, 3, 5, 6, 8$ . Williams's method yields a point of concurrence at  $x = 0.14, y = -1.55$ . The mean square for departures from

concurrence is 0.285 (2 degrees of freedom), the residual mean square ( $\text{var}(d)$ , not  $\text{var}_R(d)$ )—see Table 5) is 0.133 (12 d.f.) and  $F = 2.14$ . The present method yields (again using  $\text{var}(d)$ , not  $\text{var}_R(d)$ ),  $a = -3.75$ , i.e.  $x = 0.25$ ;  $\text{var}(\hat{y}_a) = 0.312$  (2 d.f.),  $\text{var}_E(\hat{y}_a) = 0.214$  (12d.f.) and  $F = 1.46$ . Thus, in this example, the present method yields an estimate of the point of concurrence biased towards  $\bar{x}$ , and underestimates the significance of departures from concurrence. If this reflects a general bias in the method, the significance of the results of Table 8 is enhanced.

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