

A GENETIC INVESTIGATION OF ALLOMETRIC GROWTH IN HEREFORD CATTLE¹

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BIOLOGISTS have long directed attention to problems relating to the determination of quantitative measures of body conformation and the genetic factors responsible for variation in conformation. Such variation in conformation between individual animals within a species is due to differences in the relative proportions of the various parts to each other and to the animal as a whole. D'ARCY THOMPSON (1917) pointed out that all but the simplest organisms reach their adult form by differential growth in different directions. Variation in conformation is the result of differences in relative growth rates of the various dimensions. A study of relative growth, or allometry, offers an approach to the problems of conformation.

Ramifications arising from the simple expression relating the size of a part to that of another part or the whole have been studied by investigators in the fields of theoretical and applied biology. In the present discussion reference will be made to a number of these investigations, most of which have been critically reviewed by REEVE and HUXLEY (1945), MEDAWAR (1945), and RICHARDS and KAVANAGH (1945).

The basic allometric relationship is that expressed by the equation

$$y = bx^a$$

in which y represents a part, x another part or the whole, and b and a are constants. The equation is either a parabola or hyperbola, depending on whether a is positive or negative.

In logarithmic form the equation becomes

$$\log y = a \log x + \log b, \text{ or}$$

$$Y = K + aX, \text{ where}$$

$$Y = \log y$$

$$X = \log x$$

$$K = \log b$$

Thus in logarithmic form the allometric equation is that of a straight line with slope a and Y intercept K .

Although the allometric equation had been used previously to express brain weight/body weight relations in mammals (SNELL 1891 and DUBOIS 1898, 1914) and birds (LAPICQUE 1898) as well as heart-body-weight rela-

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tions in birds (KLATT 1919), HUXLEY (1924) first used the formula to describe the relation of the growth of a part or organ to that of the whole organism and suggested that this equation might express a general law of differential growth. HUXLEY (1932) and others found a wide range of growth and size phenomena could best be described by the allometric equation.

The diverse evolution of the allometry concept has resulted in a confusion of terminology and symbolism. Recent suggestions for a standard terminology do not seem to be entirely adequate and have not been universally accepted. REEVE and HUXLEY (1945) and RICHARDS and KAVANAGH (1945) have summarized the terminology and symbolism in current use.

KAVANAGH and RICHARDS (1942) have shown that the data from most allometric studies may be classified into one of five types. These are:

Type A. Measurements of two variables X and Y are taken from time to time on the same individual and constitute the entire set.

Type B. A group of individuals as homogeneous as possible with respect to causative factors is chosen, and one set of measurements is taken on each individual. Such data actually portray relative size rather than relative growth.

Type C. A series of type B measurements is taken on the same group at successive intervals. In the usual treatment the arithmetic means \bar{X} and \bar{Y} are taken as the best representatives of the group values at each stage.

Type D. Measurements are made on a group of organisms without regard to differences between the developmental stages of the individuals, and a two-dimensional distribution is made of all the data for study.

Type E. This consists of a set of Type A curves for a group of individuals.

At present, it appears more satisfactory to give a clear statement about the class of data involved rather than a further elaboration of terminology.

KAVANAGH and RICHARDS (1942) considered several mathematical aspects of the allometric equation. They concluded: (1) the equation is dimensionally valid, a being the ratio of two specific growth rates ($dy/ydt : dx/xdt$) and, therefore, a pure number. When x is measured in U^1 and y in V^1 , the dimensions of b are $U^{-1a}V^1$. Since the value of b depends on the unit of measure, no unique biological significance or interpretation may be attached to it. (2) The relation between the parameters, $b = Be^{-ra}$, observed by HERSH (1931, 1934) is due to the mathematical treatment. (3) Contrary to LUMER's (1934) conclusions, whatever may be the curve of sigmoid growth followed by one of the variables, it is possible for the growth of the other to be sigmoid as well without invalidating the allometric formula.

HUXLEY (1924) first discovered the power equation, $y = bx^a$, empirically. Later (1932), in an attempt to establish a theoretical basis for the equation as a biological law, he derived the formula on the basis of assumptions about growth in general. A number of investigators (ROBB 1929; TWIRTY 1930; TEISSIER 1934, 1937) have postulated different hypotheses to account for the allometric equation as a fundamental law of growth, but none of these has withstood critical analysis. It must be concluded that no satisfactory theoretical basis has yet been found for simple allometry. The allometric equation

must be considered as nothing more than a statistical expression and not an intrinsic biological law of growth. The parameters of the equation cannot be given a physiological interpretation. However, the almost universal applicability of the allometric equation to relative growth data cannot be overlooked. The equation may be considered as a measure of the resultant process or processes affecting relative growth, and as such may be looked upon as a law.

The present investigation arose from the desire to discover a quantitative measure of body conformation for beef cattle that could be used as a selection criterion in a breeding program designed to produce a desired type of beef carcass. Genetic improvement of body conformation of beef cattle has progressed slowly. This is partly due to difficulties of measurement and evaluation of beef-producing qualities. An even more important cause of slowness of progress may be the fact that investigators of beef form have considered conformation as a static characteristic. Thus the heritabilities of a number of body measurements relating to beef conformation have been estimated. Most of these have been tabulated by PHILLIPS (1949).

Since body conformation at any stage of development is the result of differential growth rates of the various dimensions, genetic studies of form should take account of the dynamic processes of growth. Attention should be centered on the processes leading to the assumption of the 'specific form rather than on the end products themselves. LERNER (1939) discussed the analogous problem in poultry and pointed out that: "Genetic studies of shape or conformation which do not take account of developmental rates address themselves to the method of inheritance of something that is the result of the interaction of a number of processes rather than to the inherited factors themselves. By means of allometric constants describing growth in different dimensions, we should be able to isolate the inherited factors themselves."

HUXLEY (1932) showed that the parameters of the allometric equation provide a simple numerical basis for comparison of growth patterns of parts, organs, and dimensions. When fitted to continuous growth data the allometric equation provides a quantitative description of the relation between the parts at any stage of development over the range fitted. A number of such equations describing the relation between pertinent dimensions and body size would yield a quantitative measure of conformation. Should variation in the value of the parameters be due to hereditary differences, there could be devised a selection index, based on the parameters for quantitatively changing body conformation.

The objectives of this investigation were:

- (1) To determine whether the available relative growth data on Hereford cattle could be expressed by allometric equations;
- (2) To estimate the parameters, provided the data could be expressed by allometric equations;
- (3) To evaluate the allometric equation as a quantitative measure of body conformation; and

(4) To investigate the inheritance of the parameters of the allometric equation, thereby determining whether specified changes in conformation could be effected by using the parameters as criteria of selection.

MATERIALS AND METHODS

The animals used in this study consisted of 55 males and 52 females born in the University of California purebred Hereford herd at Davis. The data were obtained from records taken routinely as a part of the beef cattle breeding project. A series of nine measurements are taken on all animals in the herd at birth and every four months thereafter until two years of age. Subsequent measurements are made yearly until the animal leaves the herd. In actual practice the herd is weighed and measured once a month, so that there is some variation as to the exact age of each animal for each period measured.

The measurements include weight, height at withers, height at hook bones (tuber coxae), heart girth (*i.e.*, chest girth), round (distance from patella to patella parallel to the ground), length of body (horizontal distance from the point of the shoulder to the intersection with a line falling vertically from the posterior point of the tuber ischii), length of head, width of head, and width of hook bones (distance between the tuber coxae). Weight is taken on a normal fill to the nearest $2\frac{1}{2}$ pounds. Heart girth, length of body, and round are measured with a corded linen tape. The remaining measurements are taken with calipers especially designed for the purpose.

It is evident that each of the dimensions measured is the result of a combination of measurements of organs and parts. HALDANE (see HUXLEY 1932, p. 81) pointed out that if the parts of an organ (*e.g.*, segments of a limb) show unequal constant differential growth ratios against a standard, then the whole organ cannot obey exactly the allometric law against the same standard and vice versa, since the sum of a number of expressions $b_r X^{a_r}$, with different values of a_r , cannot be identical with a single expression bX^a . TEISSIER (1934) argued that since the discrepancy is slight when the values of a are not very different, the theoretical difficulty is disposed of in practice. However, it is certainly important when the biological meaning is to be interpreted.

In the present studies it was not possible to determine whether the components of each measurement show equal constant differential growth ratios against heart girth. It would, however, be an unusual coincidence if they did. Hence, it is necessary to recognize this source of error in the values of the parameters.

PRELIMINARY ANALYSIS

The requirements of the present investigation were best fulfilled by a Type E (KAVANAGH and RICHARDS 1942) analysis of the data, as this permits the study of the growth curves of individuals. Heart girth, a good criterion of body size and subject to small error of measurement, was selected as a standard with which to compare the remaining measurements. Although it may have been desirable to use a longer period, limitation of the data re-

quired the use of the range from birth through sixteen months of age. This shorter range does not affect the results seriously, as will be shown later.

In order to estimate graphically whether the data could be represented by the allometric equation a random sample of the animals was drawn, and for each a double logarithmic plot of the eight available measurements against heart girth was made. A typical set of double logarithmic plots is shown in figure 1. All the points except the first or birth measurements fell along a straight line, within the errors of measurement. It was concluded, therefore, that with the restriction discussed below the allometric equation provides a satisfactory quantitative description of beef conformation.

The first point was far out of line, indicating a disturbance in the value of a between birth and four months of age. PONTECORVO (1938, 1939) fitted the allometric equation to a foreleg length/height at withers relation in cattle and found some evidence that the most rapid growth of the trunk, relative to the foreleg, occurs just after birth. He pointed out that the young of most grazing mammals are born with relatively long limbs. Therefore, during embryonic development a must be greater than unity, and about the time of birth it assumes a value less than unity.

Measurements were taken at monthly intervals on a number of calves until they were four months of age, and a double logarithmic plot of the data was made. It was evident from these graphs that a changes markedly between birth and one month of age, but approaches a stable value after that time. The available data do not provide information as to the exact nature of this change. Further data, discussed later, indicate that a continues to change gradually throughout growth. These data suggest that a approaches at least two widely separated values during the life of an individual. Fetal values of a measure the relative growth processes that best adapt the individual to embryonic development, parturition, and early post-partum existence. Associated with the change from intra-uterine to external environment is a change in the value of a . The change is initiated during a short interval occurring just before and immediately after birth. By the time the animal reaches one month of age, a has approached a stable post-natal value.

STATISTICAL ANALYSIS

In fitting the data the first or birth measurements were omitted, since their wide divergence from the other values would influence the estimates of the parameters markedly and detract considerably from their accuracy in describing conformation. Therefore, all the parameters were estimated from four pairs of measurements corresponding to 4, 8, 12, and 16 months of age.

KAVANAGH and RICHARDS (1942) have shown that for the individual curves of a Type E analysis, the most probable values of b and a are those obtained by use of a least squares technique that accounts for error in both variables.

Theoretical justification for the use of the least squares technique arises from the condition that the errors be normally distributed and independent

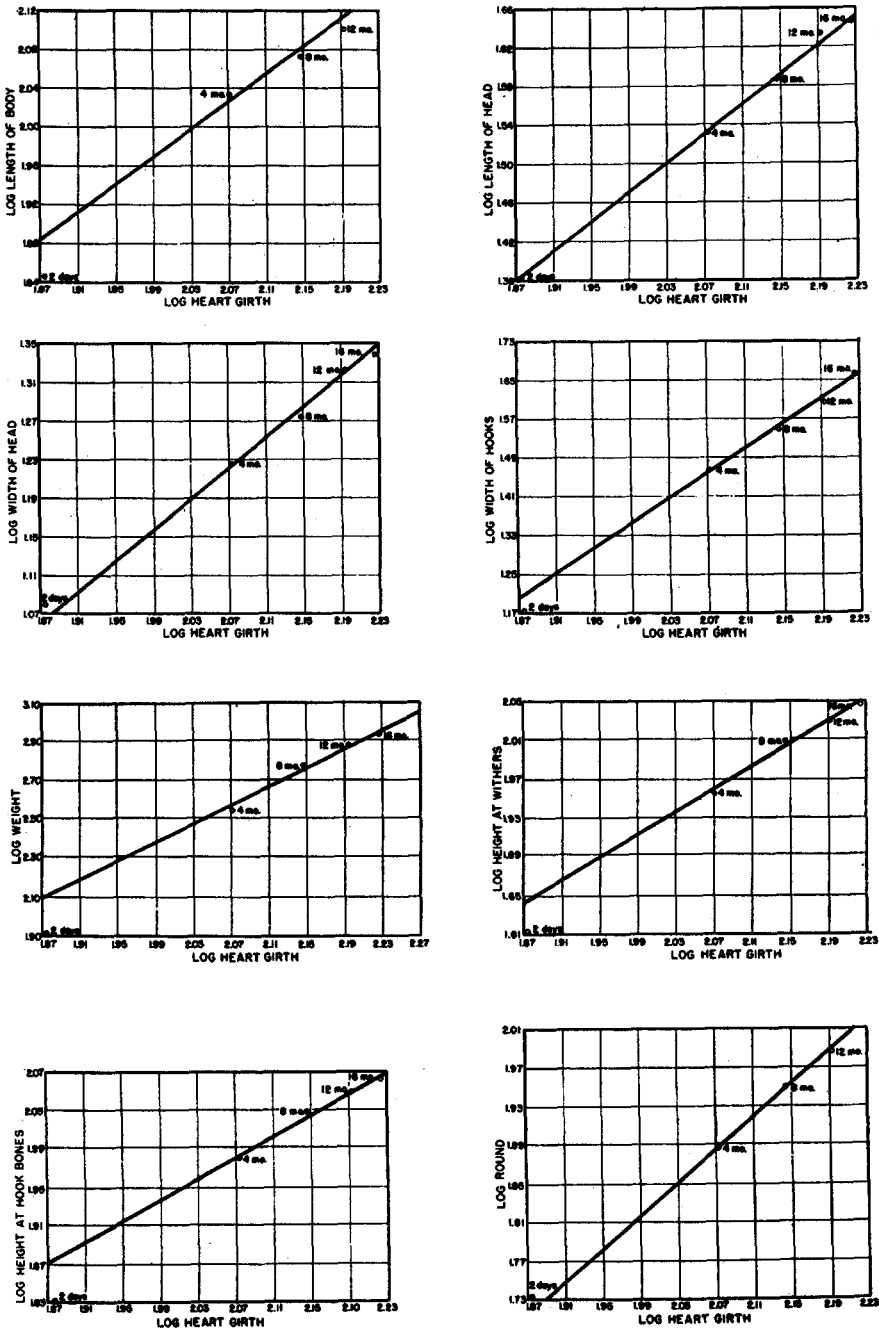


FIGURE 1.—Double logarithmic plots of eight body measurements against heart girth of a typical female.

of each other. GREGORY (1933) published the results of 100 successive measurements of the round of an individual cow. These data were tested for normality by the method of SNEDECOR (1946). The analysis indicated that the measures were normally distributed. It appears reasonable to assume that the other measurements also follow a normal distribution. Independence of the errors was assumed on the basis of the objective method of taking the measurements.

If the logarithmic form is fitted it is necessary to consider the question of weighting, since the deviations from the parabola are not equal to the deviations from the straight line logarithmic form. However, KENNY (1947) stated that the discrepancy usually does not affect the fit seriously. KAVANAGH and RICHARDS (1942) drew evidence from the data of NEEDHAM (1934) and TEISSIER (1934) and showed that there would be little difference between the correctly weighted and the unweighted methods of treatment of the logarithmic form. For the purpose of this study, the increased precision would not justify the additional labor of properly weighting the logarithmic form. The logarithms of the measures were fitted by the method of least squares to account for error in both variables suggested by KENNY (1947).

VARIATION IN a

In those instances where the data were available, parameters were estimated on the basis of six pairs of observations, *i.e.*, through 24 months of age. Comparison with those calculated on the basis of measurements through 16 months indicated that they were estimates of different parameters. The difference was not large enough to be of practical importance to the results of this investigation. It appears that the values of a and K are not actually constant, but are gradually changing throughout development. These analyses are in general agreement with those of LERNER (1938), who found variations in the differential growth rate of the leg length against body weight in the domestic fowl.

VALUES OF a AND K

Mean values of a and K are shown in table 1. The data were analyzed by means of analysis of variance to determine (1) sex differences and (2) intra-class correlations to be used in estimating heritabilities.

Significant differences in mean values of a and K between the sexes were found for height of hooks, round, width of head, and width of hooks relationships. (Height at hooks/heart girth, etc., are referred to simply as height of hooks, etc.)

Height at hooks

The data indicate that the Y intercept, K , is greater for males, but the value of a is larger for females. Thus, height at hooks has a higher relative growth rate for females than for males. At birth females are slightly higher at hooks than males of equal size of heart girth; throughout development they maintain a higher relative growth rate increasing the divergence. Simulta-

neous solution of the two equations shows that the lines intersect when heart girth has a value of 13.4 centimeters. That would occur during embryonic development. Since it has already been established that a changes markedly during the period from just before birth to one month of age, extrapolation of the data into the range prior to one month of age is not valid for purposes of biological interpretation. Thus it is clearly established that in these data a and K are not primary biological factors but possibly are measures of one. As such, they may prove useful criteria of selection.

TABLE 1
Mean values of a and K .

		Grand mean	Mean males	Mean females	Difference
Weight	a	2.660	2.662	2.657	.005
	K	-2.980	-2.976	-2.984	.008
Height at hooks	a	.571	.553	.590	.037*
	K	.789	.829	.747	.082*
Round	a	.747	.787	.706	.081**
	K	.351	.274	.432	.158**
Head length	a	.737	.749	.725	.024
	K	.004	-.020	.030	.050
Height at withers	a	.662	.614	.631	.017
	K	.653	.673	.631	.042
Length	a	.861	.854	.868	.014
	K	.220	.242	.197	.045
Head width	a	.704	.742	.663	.079**
	K	-.228	-.304	-.148	.156**
Width hooks †	a	1.162	1.110	1.223	.113**
	K	-.956	-.851	-1.078	.227**

* 5 percent level of significance.

** 1 percent level of significance.

† Means based on 48 males and 41 females.

Round

The value of the Y intercept is larger for females, but males have a greater value of a . The two curves intersect when the heart girth measures 86.4 centimeters. This corresponds to a little more than one month of age. It appears that at birth females have a greater round relative to heart girth than males, but that the males have a higher relative growth rate, so that at about one month the two sexes have the same relative size of round; thereafter the males develop a larger round, relative to heart girth, than the females.

Unfortunately, comparable data for steers are not available. However, should their growth pattern be more similar to the males than the females, it would explain in part the general preference of buyers for fat steers rather than fat heifers.

Width of head

The Y intercept is larger for females, but a is greater for males. The two curves intersect when heart girth has a value of 93.2 centimeters, which corresponds to 6 to 8 weeks of age. Thereafter, males are relatively wider of head than females, the divergence increasing until mature proportions are attained.

There is no significant difference between the two sexes as regards relative growth of head length. Males and females thus attain their characteristic different mature proportions by different relative growth rates in head width only. Thus in a group of mature animals of the same heart girth males and females would have heads of equal length, but males would have much wider heads than females.

The mean value of a for head length is 0.737 for both sexes. For head width the value for males is 0.742 and for females 0.663. As maturity progresses the ratio of head length to head width becomes progressively larger for females and smaller for males. Thus the conformation of an animal's head, *i.e.*, the ratio of length/width is in a sense a measure of maturity. This may explain why practical breeders give the shape of the head so much consideration when selecting sires or feeders. Table 2 shows how the ratio of head length over head width changes with advancing maturity in both sexes.

TABLE 2
Ratio of head length to head width for different values of heart girth.

Heart girth	Males	Females
<i>cm.</i>		
65	1.988	1.933
110	1.982	2.009
140	1.980	2.045
165	1.979	2.070
180	1.978	2.083
190	1.977	2.093
200	1.976	2.100

Width of hooks

Males have the larger intercept but females the greater growth ratio. Intersection of the curves is at a value of heart girth equal to 99.9 cm., which corresponds to an age of 3 to 4 months. Thus, at birth males are slightly wider at hooks, but the relative growth rate of the females is higher. At about 3 to 4 months the females become wider at the hooks than males of the same heart girth measurement.

EFFECT OF INBREEDING ON THE VALUE OF a AND K

In order to estimate the effect of inbreeding on the value of a and K the regression of parameter value on coefficient of inbreeding (WRIGHT 1922) was calculated in each case. The coefficients of inbreeding ranged in value from 0.00 to 0.328, with an average value of 0.073.

None of the regression coefficients were significantly different from zero at the 5 percent level. Insofar as the limited data can be interpreted, there is no evidence of any effect of inbreeding on allometric growth in the population.

INTRA-CLASS CORRELATION ANALYSIS OF a AND K

Intra-class-half sib correlations for a and K were determined by analysis of variance and are shown in table 3. Sex differences were found for height at hooks, round, head width, and width of hooks relationships. The sex difference between values of a for round was just significant at the 5 percent level, the remaining differences being non-significant. A biological explanation of this difference is not immediately apparent. Since, with the ex-

TABLE 3
Values of half-sib intra-class correlations.

	Males		Females		Both sexes	
	a	K	a	K	a	K
Body weight					.10	.10
Height at withers					.16*	.16*
Height at hooks	.28**	.28**	.25*	.26*	.25 ² ,***	.25 ² ,***
Length					.16*	.15*
Round	.18*	.17	-.06	-.04	.08 ²	.07 ²
Length of head					.31**	.32**
Width of head	-.13	-.13	.06	.07	-.02 ²	-.02 ²
Width of hooks ¹	.15	.17	.15	.15	.13 ² ,*	.13 ² ,*

¹ Means based on 41 females and 48 males.

² Pooled values for sexes based on method of combination described by WHATLEY (1942).

* Significant at 5 percent level.

** Significant at 1 percent level.

ception mentioned, the differences noted between sexes were not significant the data for the two sexes were combined by the method described by WHATLEY (1942).

The value of the correlation for a and K for round measurement and head width is not significantly different from zero, and that for weight is just short of the 5 percent level of significance. The remaining correlations are all significantly different from zero—those for height at hooks at the 1 percent level and those for height at withers, body length, length of head, and width of hooks at the 5 percent level.

ESTIMATES OF HERITABILITY OF a AND K

The average genetic relationship among all half sibs in the population is 0.326. Heritabilities were estimated by multiplying the values of the intra-class correlation by the reciprocal of the average genetic relationship. These estimates are given in table 4. Significance of these estimates is determined by the significance of the intra-class correlation. WHATLEY (1942) pointed

out that there is very little dominance or epistatic correlation in heritability estimates obtained in this way. However, the small number of sires involved gives rise to a large sampling error.

Errors in estimates of heritability in either direction cannot be recognized with certainty unless they are less than zero or greater than unity. The estimates for head width and head length are apparently both in error. The heritabilities of a and K for head width are probably zero, while those for head length are quite high. It is puzzling that the variability of the relative growth rate of width of head is not at all influenced by additive gene action, but that variability of length of head is due almost entirely to additive gene action.

The generally high value of the heritability estimates is at variance with the results of investigations with the domestic fowl. LERNER (1943) summarized the results of four generations of progeny test selection involving 320 offspring for high and low values of a in a tarsometatarsus/body weight comparison and concluded that the genetic variability of the relative growth pattern in the stock used was either non-existent or so low as to preclude its demonstration by the method of selection in opposite directions employed.

TABLE 4
Heritability estimates.

	Weight	Height at withers	Height at hooks	Length	Round	Head width	Head length	Width hooks
a	.30	.50*	.75**	.48*	.23	-.08	.96**	.40
K	.32	.50*	.77**	.45*	.23	-.06	.97**	.40

*Significant at 5 percent level.

**Significant at 1 percent level.

LERNER's comparison was made with weight as a standard of body size while heart girth was used in the present investigation. The estimates of the half-sib correlation of a and K for the weight/heart girth relation were just short of the 5 percent level of significance, and thus it is questionable whether the actual heritability differs from zero. This suggests that relatively large measurement errors and random fluctuation in weights (as contrasted with linear measurements) might increase the environmental portion of variance of a and K to the extent that heritability of a and K becomes so low as to preclude its demonstration. It was, in fact, consideration of this possibility that led to the use of heart girth as a standard of body size in this investigation.

The hypothesis that heritability of a and K would be low or zero when body weight was taken as the standard was tested. The heritabilities of a and K for height at hooks are 0.76 and 0.77 respectively. Heritabilities for a and K for a height of hooks/weight relation were computed. In this instance a least squares technique accounting for error in one variable only was used to estimate a and K . This method used by LERNER increases the environmental portion of the variance of the parameters. The heritabilities of a and

K thus computed were not significantly different from zero. It would therefore seem that weight is not a satisfactory measure of body size when used as a standard for allometric growth studies, which may account for LERNER's failure to obtain gains under selection.

RELATION BETWEEN a AND K

The question of possible mathematical relationships between the parameters has been considered. HERSH (1931, 1934) observed the relation $b = Be^{-ra}$ in the values obtained from his study of facet number in bar-eyed *Drosophila* and in a study of relative size in various species and genera of titanotheres. In this equation B and r are constants and e is the base of the natural logarithms. LUMER (1936) pointed out that this relation is the necessary and sufficient condition that the relative growth curves shall all pass through a common point. KAVANAGH and RICHARDS (1942) studied double logarithmic plots of HERSH's data and pointed out that because of the unit of measure and because the organs measured were all of roughly comparable size, the points were grouped in a fairly small area of the plane compared with the distance to the line $X = 0$. Since the numerical value of K is the value of Y when $X = 0$ determination of K from the data represents extrapolation a considerable distance beyond the data and an approximation to LUMER's condition that all lines pass through a common point. The distance to the line $X = 0$ depends on the unit of measure of x . The line $X = 0$ can be moved closer to or even into the group of points by taking a larger unit of x and as the degree of extrapolation diminishes or disappears the relation between the parameters vanishes. KAVANAGH and RICHARDS (1942) present a rigorous mathematical demonstration of these arguments.

The relatively small unit of measure of x (heart girth in centimeters) employed in this study results in an extreme degree of extrapolation, and a close approximation to LUMER's condition that all lines pass through a common point. As a consequence, K is largely an inverse measure of a and most of the variation in K is merely a magnified inverse of the variation in a . This is illustrated by the close similarity between values of the half-sib correlation for a and K (table 3). Phenotypic, genetic, and environmental correlations between a and K were estimated. The phenotypic correlations were calculated directly from the raw data, and the genetic and environmental correlations were evaluated by the method of covariance analysis described by HAZEL, BAKER and REINMILLER (1943). These correlations all approached or were actually estimated as -1.0 as would be expected. It can be concluded therefore, that a and K are measures of the same biological phenomenon when determined by a type E analysis employing a relatively small unit of measure of x . These observations differ from KAVANAGH and RICHARDS (1942) conclusion that, since the value of b depends on the unit of measure no unique biological significance or interpretation may be attached to it. Since the actual value of b or K depends upon the unit of measure it is necessary that the same units be used for different values of K to be comparable. With this restriction it would seem that both a and K are valid measures of the same underlying

biological phenomenon. Practical consequences of this condition with respect to selection will be discussed later.

DISCUSSION

The relative growth data analyzed in this study can be represented by allometric equations. There are, however, some limitations that should be considered in order to interpret the biological significance of the results.

WRIGHT (1918, 1932), NELSON and LUSH (1950) and others have concluded from studies of inheritance of body size that the greater part of variation in a measurement within a race or breed is due to general size factors, *i.e.*, factors which affect all parts of the body approximately proportionately, and only a small portion of it is due to special or group factors. Wide differences in relative proportions or conformation within the Hereford breed are obvious, and it follows that they must have resulted from differential growth in different directions. The generally high heritability estimates obtained in this study indicate that some of these variations are in part the result of additive gene action. It should be emphasized, however, that the allometric equation when fitted to relative growth data of the type used in the study, exclude virtually all differences in general size. Therefore, it is necessary to consider the problem of general size independently but simultaneously with that of relative size. This is particularly true as regards selection practices.

The equation was fitted to Class E data as defined by KAVANAGH and RICHARDS (1942). Theoretically the allometric equation can be considered as adequately describing the relationships only when the discrepancy between calculated and observed values is within the limits of measurement error. Inspection of a number of graphs indicates that for the range fitted (4 through 16 months) this requirement is fulfilled and that the allometric equation provides a satisfactory description of beef cattle conformation. There is evidence that this condition would not hold over a longer range. First, there is the marked change observed in the value of a between birth and one month of age. There is also the observed difference between values of a calculated on the basis of 4 months through 16 months and those calculated on the basis of 4 months through 24 months. This difference indicates a changing value of a , so that any extrapolation beyond the range fitted will not give an exact representation of the relationships. The discrepancy will not be so marked if one extrapolates into the range between 16 months and maturity, but will be more serious as one extrapolates beyond the lower limit at one month.

Although these limitations make a physiological interpretation difficult, they do not lessen the usefulness of the equation for describing conformation. The description is nearly exact over the range fitted. The equation describes the relation between the two dimensions at any given time during development and the changes that take place during development. It is possible, by suitable combinations of the equations, to describe three-dimensional relationships and changes through any desired planes. It is also possible to compare any two measurements directly by eliminating the common standard, or to study changes in the relation between two of the measurements as the stand-

ard changes during maturity. Thus, the allometric equation, fitted to relative growth data, would appear to give a satisfactory quantitative description of conformation.

A major objective of this study was to determine the usefulness of the allometric equation as an aid in selection for changes in conformation. Since it has been demonstrated that the allometric equation is adequate for a quantitative description of conformation, the problem is reduced to determining whether the parameters can be modified by selection. In order to gain information on this point estimates of the heritabilities of each of the parameters were made. The data were amenable to the half-sib correlation method used.

Heritabilities of a and K for three of the relations were not significantly different from zero. For two of these, weight and round measure, it would appear that environmental contributions to the total variability are so large as to reduce the heritability. Both weight and round are influenced markedly by the plane of nutrition, while the effect on bone growth is not so great. This would be a source of much of the environmental variability.

The head relationships are puzzling. Heritability of the parameters for head width are almost certainly zero, while heritability of head length is estimated at unity. It seems hardly reasonable that such an outcome could be due to sampling error. It is more likely that the results are due to some peculiarity of the development of the bones of the skull.

In 1934 BRASH (see REEVE and HUXLEY 1945, p. 135) concluded from his studies with madder-feeding that increase in size of the skull is due primarily to external surface accretion and internal surface absorption rather than to growth of the ends of individual bones.

It seems, therefore, that no simple concept of multiplicative or additive growth can be applied to explain changes in skull proportions; nevertheless, the data for head dimensions appear to fit the allometric equation as well as the data for the other dimensions. One obvious and important result of differences in heritability of relative growth rates of the two dimensions of the head is that any change in conformation of the head must be effected by a change in length only, even though the factors controlling sexual dimorphism of head shape operate on width alone.

The heritability of the parameters of the remaining comparisons indicates that considerable change in conformation could be effected by selection for high or low values of the parameters. The data indicate that the parameters of the allometric equation would be useful criteria of selection for changes in body conformation in those instances where comparisons are between measures of linear skeletal development. In instances where muscular and fatty tissues are involved, it would be necessary to maintain a uniform plane of nutrition and to keep the environmental factors as nearly constant as possible. If this could be accomplished satisfactorily, the parameters of the allometric equation expressing such relationships might be usable as criteria of selection.

As previously indicated, the fact that a and K are measures of the same biological phenomenon gives rise to certain practical consequences with respect to selection. The relationship between a and K cannot be modified by

selection, *i.e.*, selection for one parameter will elicit or automatic correlated response in the other. Thus, it will not be possible to increase or decrease the value of K without a correlated decrease or increase in a . Although it is not possible to change a - K relationships by selection, it is possible to modify the a - K complex by selection either for a or K . Thus selection for either parameter alone is as effective as selection for both. Ease and simplicity of determination and manipulation will dictate the choice in any particular instance.

These considerations suggest the possibility of using a simple ratio taken at a standard body size as a criterion of selection. A simplification of this type would aid materially in actual breeding programs. The generally high heritabilities for various body measurements reported in the literature (PHILLIPS 1949) would lend support to the possibility of using a simple ratio. However, a simple ratio, or single plot, does not define a unique estimate of either parameter, and therefore it is not possible to determine the pattern of relative growth. A single ratio, therefore, would not be a suitable criterion of selection.

At least two points must be measured to define a unique genotype for the a - K complex. The minimum number of observed points compatible with the required degree of accuracy must be determined in each instance. In this connection, it is also necessary to consider the optimum age at which to practice selection. From the standpoint of the practical breeder the problem is to determine the minimum number of observations and the earliest age range over which to take them. A detailed analysis of this question was not possible, but several pertinent points are worthy of mention.

The nature of the change in value of a throughout growth should be investigated. Unless the change is marked, the effects will be small. Possibly a more important factor in determining the minimum number of points required is the effect of a reduced number of observations on the heritability estimates of a and K .

The degree of maternal effect involved in the inheritance of the parameters also has a bearing on the optimum time at which selection should be practiced. The half-sib correlation method used to evaluate heritability in this study does not include maternal effects, and sufficient data are not available at present to estimate them. However, the possibility of the existence of maternal effects cannot be overlooked. If present, maternal effects would reduce the rate of gain expected from mass selection and progeny testing.

SUMMARY

An investigation was made to determine whether relative growth data obtained from the University of California purebred Hereford herd could be represented by the allometric equation. The data consisted of a series of nine body measurements taken at birth, 4, 8, 12, and 16 months on 55 male and 52 female progeny of ten sires. The measurements include weight, height at withers, height at hooks, heart girth, round, length, width of head, length of head, and width of hooks.

Heart girth was selected as a standard of body size, and each of the remaining dimensions compared with it in a series of Type E allometric equa-

tions. For all such comparisons the value of a changes markedly between birth and one month of age. After that time it remains nearly stable, changing only slightly.

It was found that the data could be represented by the allometric equation over the range fitted and that the parameters give a simple numerical description of the relative growth patterns of the dimensions studied. The allometric equation provides a satisfactory quantitative description of body conformation.

A sexual dimorphism in relative growth pattern was noted for height at hooks, round, head width, and width at hooks. It was found that with advancing maturity the ratio of head length to width becomes progressively smaller for males and larger for females. It is suggested that this ratio may be a criterion of rate of maturity.

Heritability of a and K was estimated by the half-sib correlation method. These estimates indicate that in many cases the parameters of the allometric equation can be changed by selection. In general, the parameters of equations relating linear skeletal dimensions are heritable to a higher degree than those involving muscular or fatty tissues.

The heritabilities of the parameters for width of head did not differ from zero, but those for length of head were very highly heritable. An explanation is not immediately apparent.

An inverse mathematical relationship exists between the parameters. The practical consequences of this relation are that it is not possible to change the relationship between a and K by selection, but that it is possible to change the a - K complex by selection for either parameter alone.

It may be concluded that the allometric equation offers a quantitative description of beef cattle conformation, and that conformation might be changed in a specific manner by selection for desired values of the parameters.

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