Genetical studies on growth and form in the fowl

2. The complexity of changes in skeletal proportions produced by selection

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1. INTRODUCTION

If a population is selected for some measure of size at a particular age, it is to be expected (*a*) that the changes in size at other ages will not always be proportionate, and (*b*) that not all parts or tissues of the body will be equally affected. Equally, if selection is practised for some measure of shape, it is to be expected (*a*) that the resultant changes will not be equally expressed at all ages, and (*b*) that other aspects of shape, besides the one directly selected for, will be altered.

Changes of this kind may be regarded as at least partly due to pleiotropism, but in situations such as this pleiotropism of some kind is to be expected from the very nature of the case. The problem is rather to predict and to understand the precise nature and extent of the pleiotropic changes in a particular instance. The changes may also be expressed in terms of genetic correlations, but to estimate the genetic correlation between size or shape at two different ages, or between two different bodily dimensions (as has been done, for example, by Siegel, 1963; Johnson & Asmundson, 1957), while it may be a useful guide to the applied breeder, does not throw any appreciable light on the biology of the situation.

Numerous attempts have been made (see Cock, 1966; Gould, 1966, for references), using various techniques of multivariate analysis, to analyse variation in size and shape at a given age into a number of more-or-less independent components. These have met with varying degrees of success in different instances and species. Since the underlying causes of variation are undoubtedly to a large degree developmental and genetic in nature, a deeper insight should be gained if (*a*) the multivariate analysis is combined with an ontogenetic analysis, and (*b*) the population analysed consists of a number of strains which have been selected in known ways, rather than a random sample from a single, more-or-less unselected population.

Very few studies fulfilling either of these criteria have been published. Robertson & Reeve (1952) have selected lines of *Drosophila melanogaster* for long or short wings or thorax (two selected lines from different foundation strains in three of the four selection criteria) and have compared the correlated changes produced in the unselected dimension. The comparisons have been expressed by Reeve (1950) in terms of 'coefficients of genetic allometry', i.e. the percentage (or logarithmic)

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change in the unselected dimension, divided by the percentage change in the selected dimension. For upward selection for wing length and downward selection for thorax length the coefficients of genetic allometry were high: 1·0–1·1. For the other two combinations, the coefficients of genetic allometry were much lower: 0·5–0·7. Thus in each instance, thorax length responds more readily to upward selection, whether direct or indirect, while wing length responds more readily to downward selection. It should be noted that the coefficients of genetic correlation between thorax length and wing length were very similar—about 0·7—for both upward and downward selection. This provides a good illustration of the limitations of genetic correlations in this context: they do not contain all the relevant information about correlated responses.

Robertson (1962) has selected lines of *Drosophila melanogaster* for high and low values of the ratio wing length:thorax length, eventually, after 10 generations, achieving a difference of 30 % in this ratio. Nearly the whole of this difference was due to changes in wing length: the selected lines were nearly identical in thorax length. The most interesting aspect, for present purposes, of Robertson's results is that the changes in wing length were accompanied by changes in leg length, a character not subjected to direct selection. When corrected by regression analysis for the slight differences in thorax length, the tibial length was 5·4 % greater in the upward selection line (average of all three legs, under two sets of environmental conditions). There is thus a positive genetic correlation between wing length and leg length, independent of thorax length. Further evidence on rather similar lines is provided by the studies of Misra & Reeve (1964) on geographical races of *Drosophila subobscura* and *D. robusta*. They found that wing length and leg length tended to vary together, in contrast to head width and thorax length. The studies discussed in this and the preceding paragraph have all been carried out on holometabolous insects: the differences are therefore presumably due to differences in the initial size and/or growth rates of the imaginal disks, but no specific information on this aspect is available.

2. MATERIAL AND METHOD

The results to be reported here relate to measurements on prepared adult skeletons from four selected lines of fowl. The lines, all derived from the same cross-bred foundation population, are: High Index (HI), Low Index (LI), High Weight (HW) and Low Weight (LW). HW and LW were selected respectively for high and low live body weight at 10 weeks of age. HI and LI were selected for high and low values of an index of relative shank length, *i.e.* log (shank length) − 0·4 log (body weight), both measurements again being made at 10 weeks of age. The coefficient 0·4 in the index is the approximate average value of the coefficient of ontogenetic allometry during postnatal growth up to 10 weeks (Cock, 1963*a*). The term shank length is used to denote the external live measurement, so as to avoid confusion with the measurement on the dried skeleton to which it most nearly corresponds, namely tarsometatarsal length. The externally measured distance includes, besides

the length of the tarsometatarsus, the thickness of the distal end of the tibiotarsus, but there is no doubt that differences in tarsometatarsal length account for all but a small fraction of the variation in shank length. The average age at sexual maturity in these stocks was, very roughly, 20 weeks, so that selection in all the lines was exercised upon juveniles which were about half-grown. Ontogenetic aspects of the selection responses have been briefly discussed elsewhere (Cock, 1963*b*, 1966).

The skeletons are all of females which had been selected for breeding; they are thus not random samples of their respective selected generations, but rather more extreme. All come from the third selected generation, and are nearly equally distributed between two hatches. The HW and LW birds, however, are not contemporary with those of HI and LI, since selection of HW and LW was begun 1 year later. (This introduces an additional and unknown source of error into comparisons between the two pairs of lines, i.e. HI or LI versus HW or LW. Both size and shape are known to be subject to 'hatch effects' (Cock & Morton, 1963, and unpublished results). Such effects, however, are usually small and unlikely to be seriously misleading in the present instance.) The birds, all over 12 months old when killed, were boiled, the skeletons were partly disarticulated and roughly cleaned, and then incubated in a suspension of papain in water at 38 °C for about 36 h. The bones were then cleaned, bleached in hydrogen peroxide and air-dried.

Measurements of bone lengths (and all measurements exceeding 2 cm) were made with parallel-jaw vernier callipers to 0·1 mm. The anatomical points between which measurements were taken were generally those specified by Hutt (1929). Measurements of the shaft thickness of long bones were made with a screw-micrometer to 0·01 mm. With a few exceptions (carpometacarpus, scapula) the point at which thickness measurements were taken was the mid-point, determined by laying the bone along a transparent scale lying on a mirror. Both the maximum and minimum thickness at this point were measured. It had originally been intended to combine these into a single estimate of cross-sectional area. It became evident, however, that for some bones the maximum and minimum thicknesses were behaving differently: the two have therefore been treated throughout as separate variables. For paired bones, the means of the measurements on right and left sides have been taken. In a few instances fragments of broken bones have been glued together, or measurements have been estimated from slightly damaged bones. Some measurements, notably sternum length, which might have been desirable have had to be omitted because many of the bones were irreparably damaged. All the measurements listed in Table 1 were made on all 53 available skeletons (15 each of HI and LI, 12 of HW and 11 of LW).

Selection for weight is regarded here as having been essentially selection for *general* size, irrespective of any differences in shape. Index selection, on the other hand, was designed to act upon a particular type of variation in shape, while avoiding (or at least minimizing) any direct selection for general size. In comparing HW with LW, the main focus of interest is how far selection for size brings about proportionately equal changes in the various parts of the skeleton, and, if there are

Table 1. *Means of measurements in the four selected lines*

(HI (high index), LI (low index), HW (high weight) and LW (low weight). All linear measurements in mm.; weights in g.)

	Length				Width — Thickness (max.)				Depth — Thickness (min.)			
	HI	LI	HW	LW	HI	LI	HW	LW	HI	LI	HW	LW
Femur (Fem.)	94·3	84·5	93·8	78·8	9·53	9·47	9·95	8·61	8·40	8·26	8·67	7·63
Tibiotarsus (Tib.)	136·4	119·2	134·1	113·2	8·69	8·84	9·24	7·68	7·60	7·48	7·64	6·65
Tarsometatarsus (Tmt.)	94·1	76·4	89·2	75·9	8·72	9·06	9·05	7·72	6·41	6·07	6·62	5·45
Humerus (Hum.)	85·3	78·6	85·7	73·9	9·12	9·22	9·31	8·44	7·50	7·45	7·69	6·90
Radius (Rad.)	75·7	69·0	75·1	63·7	3·92	4·23	4·15	3·64	3·13	3·27	3·32	2·88
Ulna (Uln.)	83·9	76·9	83·1	70·8	7·35	7·55	7·68	6·77	5·17	5·33	5·41	4·75
Carpometacarpus (Cmc.)	46·5	42·6	45·9	39·9	11·33	11·67	11·67	10·10	5·07	5·30	5·18	4·56
Coracoid (Cor.)	66·1	60·5	66·0	55·7	7·38	7·24	7·88	6·58	5·44	6·10	6·40	5·18
Scapula (Sca.)	84·8	79·8	85·7	72·3	8·83	8·87	9·26	8·12	2·29	2·64	2·61	2·10
	Length				Width				Depth			
	HI	LI	HW	LW	HI	LI	HW	LW	HI	LI	HW	LW
Synsacrum (Syn.)	105·1	97·6	105·7	90·2	65·8	63·6	65·6	54·9	—	—	—	—
Sternum (Ste.)	—	—	—	—	39·7	39·0	42·7	36·5	35·9	34·6	38·6	33·6
Clavicles (Cla.)	53·7	50·6	54·9	49·3	37·1	36·8	39·6	34·2	—	—	—	—
Cranium (Cra.)	44·6	43·8	45·3	41·0	28·2	28·1	29·2	26·7	23·4	23·1	24·0	22·2
Lower jaw (Jaw)	62·4	57·7	62·7	54·7	30·7	31·4	33·0	28·5	—	—	—	—
	Weight											
	HI	LI	HW	LW								
At 10 weeks	895	1032	1168	696								
At 20 weeks	1811	1997	2302	1316								
At death	2705	2572	2687	1414								

unequal changes, what particular pattern they display. Comparisons between HI and LI raise such questions as the extent to which shape selection utilizes genes which change specifically the length of the tarsometatarsus (but not the lengths of the other leg bones) or change the size of the leg as a whole (but not of the wing), and so on. To investigate questions of this kind in a comprehensive and systematic manner would demand some form of multivariate analysis. In the present instance, however, the differences between the lines are so great that a good deal can be learnt by less sophisticated methods.

Table 2. *Mean differences in various anatomical groups, and in body weight, expressed as percentage deviations from the control values* $(HW + LW)/2$

(*n* = number of measurements. Groups 3 and 4 include all the limb bones, plus the coracoid and scapula. For further explanation, see text.)

	n	HI	LI	HW
1. Lengths of leg bones	3	11·2	− 4·4	8·4
2. Lengths of wing bones	4	8·4	− 0·7	7·7
3. Lengths of all long bones	9	9·2	− 1·7	8·1
4. Thicknesses of all long bones	18	2·1	4·8	7·5
5. Lengths of median bones	4	5·0	− 0·9	6·2
6. Widths and depths of median bones	7	1·8	0·4	7·1
7. Weights				
At 10 weeks	—	− 4·0	10·7	25·7
At 20 weeks	—	0·1	10·4	27·2
At death (> 60 weeks)	—	31·9	25·4	31·0

In Table 2 and Fig. 1, the mean values of the measurements in each line (themselves given in absolute terms in Table 1) are expressed as percentage deviations from a 'control' value. No control population in any strict sense (e.g. unselected descendants of the original foundation stock) is available. A 'hypothetical control' has therefore been constructed, taking the arithmetic means of the values of HW and LW. No particular virtue is claimed for this as a standard of comparison: it is a compromise between the needs to facilitate a number of different kinds of comparisons. Other control standards (e.g. the mean of all four lines) could have been used with as much (or as little) justification: in all the most important respects (that is, differences between lines, rather than the deviations of single lines from the controls), they would have yielded closely similar results. Too precise a meaning should not, therefore, be read into the control standards. For example, many of the measurements in LI deviate only very slightly from the control values: this does not necessarily indicate that these measurements have changed only slightly under downward selection for the index. There is no particular reason to expect that responses to selection in opposite directions (whether direct responses or collateral ones) will have been symmetrical. In at least one respect there is clear evidence (from other, unpublished data) that the response has been strongly asymmetrical: weight has responded much more rapidly to downward selection (in LW) than to upward selection (in HW)—compare Falconer (1964, p. 199) for a similar result in mice.
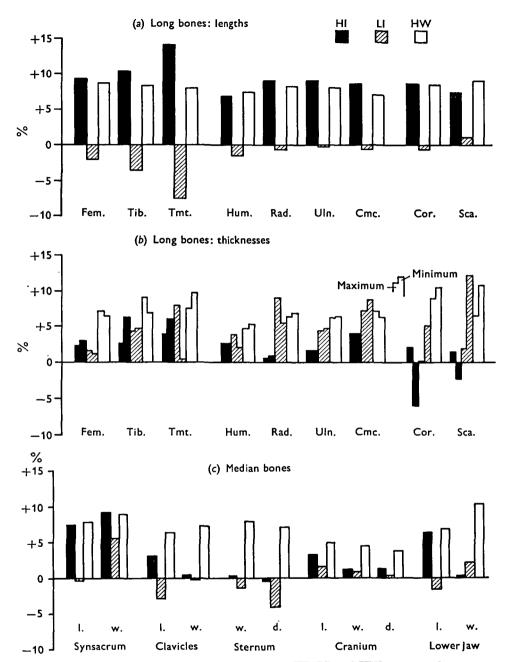
Fig. 1. Means of skeletal measurements in lines HI, LI and HW, expressed as percentage deviations from $(HW + LW)/2$, which is taken as a 'control' value. In section (b) the left part of the column for each bone and line indicates the maximum thickness, and the right part the minimum thickness. For key to abbreviated names of the bones, see Table 1; l = length, w = width, d = depth.

Values for LW are not given separately in Table 2 and Fig. 1: they are, as a matter of arithmetical necessity, identical with those for HW, but of opposite sign. It should also be kept in mind that whereas the total divergence under shape (index) selection is the difference (taking sign into account) between the values for HI and LI, the total divergence under size (weight) selection is *twice* the value given for HW.

In Table 2 an attempt has been made to render the wood more readily distinguishable from the trees by grouping together those measurements which have a similar anatomical nature. The first two groups—lengths of leg and of wing bones call for no further explanation or justification, but some of the other groupings are in some degree arbitrary. Group 3—lengths of all long bones—contains, besides the seven limb bones, two bones (coracoid and scapula) of the pectoral girdle. The reason for including these with the limb bones is their elongate shape with articular surfaces at one (scapula) or both (coracoid) ends, and that their transverse measurements are best described as 'thicknesses', rather than (as with the other components of the limb girdles) as 'widths' or 'depths'. Groups 3 and 4 thus relate to the same set of bones. It is arguable, however, that it would have been at least as logical to have excluded the scapula and coracoid, transferring them instead to group 5, which could then have been renamed 'lengths of bones of the trunk and head'. In the event, the figures resulting from such a regrouping show only trivially small differences from those given in Table 2.

3. RESULTS

The following points, *inter alia*, emerge from examination of Tables 1 and 2 and Fig. 1.

(1) Comparing the lengths of the leg bones in HI and LI, there is a very marked gradient: HI exceeds LI by 21·4 % in the tarsometatarsus, 13·8 % in the tibiotarsus and only 11·4 % in the femur. The statistical significance of this gradient is beyond doubt, as is shown by an analysis of the individual values of the ratio: tarsometatarsus length/femur length. The mean values are 0·988 for HI and 0·904 for LI; $t_{28} = 11·0$, $P \ll 0·001$. There is in fact no overlap between the two lines in the individual values of the ratio. Clearly, much of the selection as between HI and LI has been directed towards a specific elongation in HI (or shortening in LI) of the tarsometatarsus. HW and LW are both intermediate in this respect, suggesting that selection has been effective in both directions. It should be noted that in HW, as compared with LW, the difference in length declines slightly in a distal direction. In other words, the coefficient of *genetic* allometry, under selection for size (weight), is very slightly lower for the more distal bones. This is the reverse of the effect found by Lerner (1936, 1937) in embryonic and post-natal growth: the coefficient of *ontogenetic* allometry increases distally. For other instances where corresponding coefficients of ontogenetic and static allometry differ, see Cock (1966) and Gould (1966).

(2) The differences between HI and LI in lengths of the wing bones are less than

in the leg bones. Thus a (comparatively small) fraction of the response to shape (index) selection consists of an elongation of the leg as a whole, relative to the length of the wing. It might be preferable, so as to exclude effects operating specifically on the distal end of the leg, to compare the wing with the femur alone. In that case the extra $HI - LI$ difference in the leg is even smaller: 2.3% (11.4% in the femur, minus 9.1% in the wing). Another, and rather more surprising, feature is that in each of the four main wing bones the difference between HI and LI is very nearly equal. There is thus no sign of any proximo-distal gradient of elongation in the wing, such as is found in the leg. In view of the serial homology between leg and wing one would have expected that at least some of the genes responsible for specific elongation of the tarsometatarsus in HI would have had a similarly specific effect on the carpometacarpus (as compared with other wing bones). This appears not to be the case or, at least, any such effect is too slight to be separately discernible.

(3) HI exceeds LI in all the 13 measures of length (average = 9.4%): in the seven measures of width and depth the excess is markedly less (average = 1.4%), while in most of the 18 thickness measurements LI exceeds HI (average = -2.7%). Thus LI clearly has a much more compact and thickset conformation than HI, with a relatively deeper and wider body, and shorter and thicker limbs. This difference is, to some extent, of a similar nature to the ectomorph–mesomorph type of variation in human physique (Sheldon, 1940; Tanner, 1962), HI being ectomorphic and LI mesomorphic. The greater *general* size of HW is reflected in the fact that it is consistently larger than HI in measures of median bones (average = 3.8%) and of thickness (average = 5.4%). In contrast, HW is slightly smaller than HI in measures of length of the long bones (average = -1.1%). HW is thus intermediate between HI and LI in the ectomorphy–mesomorphy component: LW is, in this respect, similar to HW.

(4) In certain bones the changes in maximum and minimum thickness are widely disparate in the different lines. The most striking instances occur in comparisons of HI with LI. In the tarsometatarsus LI shows a greater increase in maximum thickness than HI, whereas in minimum thickness HI shows a greater increase than LI. Thus LI has a much flatter cross-section than HI. Conversely, in the coracoid and scapula, HI has a flatter cross-section than LI. The statistical significance of these comparisons has been tested by calculating the maximum/minimum ratios of individual birds and applying a t-test. The results ($t_{28} = 5.2$, 6.4 and 4.0 respectively for tarsometatarsus, coracoid and scapula) show that all the differences are highly significant at $P < 0.001$. HW tends to resemble HI in the tarsometatarsus, and LI in the coracoid and scapula: thus in all cases it resembles the line with the less flattened cross-section.

(5) Differences in cranial shape between the four lines are slight: in decreasing order of size the lines rank HW, HI, LI, LW in all three dimensions. There is a slight but consistent tendency for length to show greater increases than width, and width than depth. However, although HI is only 1.8% above LI in cranial length, it is 8.8% above LI in length of lower jaw, indicating that the nasal and beak

region is disproportionately elongated relative to the cranium. A *t*-test on the individual cranial length/jaw length ratios shows this difference to be highly significant ($t_{28} = 6.5$, $P < 0.001$). HW resembles HI rather closely in this respect, whereas LW is similar to LI.

(6) If we compare HW with LW (remembering that values for LW are the same as for HW, but with a negative sign) in respect of all the measurements, the general impression is one of uniformity. Most measurements show HW some 12–18 % larger than LW. A few measurements depart from this general uniform trend: some of these have already been discussed. The impression of uniformity is reinforced if, as in Table 2, the measurements are combined into groups according to their anatomical nature. Thus, as might have been expected from the kind of selection applied to the HW and LW lines, the general picture is overwhelmingly one of a large difference in *general* size, with some relatively slight differences in shape superimposed upon it. The figures for body weight (Table 2) are in agreement with this: differences of 12 % and 18 % in linear measurements correspond to differences of 40 % and 64 % in a cubic measurement, and the differences in weight at the different ages are within these limits. The three cranial measurements yield differences between HW and LW which are (with the sole exception of maximum thickness of humerus) smaller than those for any other measurement. The cranium is thus less affected by changes in general size than are other parts of the body. This is in agreement with the results of Jerison (1955), who found that, between mammalian species covering a very wide range of sizes, brain weight increased approximately as the 2/3 power of body weight.

(7) The most striking feature of the figures for body weight is the behaviour of HI. From being, at 10 weeks, lighter than LI and HW it progresses to become, at killing, substantially heavier than LI and slightly heavier than HW. The excess over HW is probably an accident of sampling: at ages beyond sexual maturity weight becomes subject to large fluctuations, depending on recent laying history, amount of stored fat, etc. Moreover, the samples of HW and LW were killed at a different season from those of HI and LI: February and June–July respectively. However, other unpublished evidence concurs in indicating that HI catches up with, and eventually overtakes, LI in weight. There are, besides, two other pieces of evidence which support the view that HI is a comparatively late-maturing line. The first is that the lower weight of HI at 10 weeks is entirely due to a lower rate of growth in weight during the first 2 weeks after hatching: at ages beyond 2 weeks the (logarithmic) growth rate is very slightly higher than in LI. The second is that HI females reach sexual maturity (judged by the age at which the first egg is laid) about two weeks later than LI contemporaries.

4. DISCUSSION

The four lines have been shown to differ among themselves in a general size factor (with HW and LW occupying the extreme positions) and at least six distinct and independent shape factors, in all of which HI and LI occupy the extremes.

These are (1) a factor increasing the length of the leg-bones (relative to the rest of the body); (2) a factor increasing the length of the tarsometatarsus (or, more generally, the distal end of the leg); (3) one increasing the thickness of the long bones in general (including the coracoid and scapula). Next are factors affecting the degree of flatness or roundness of cross-section of the shafts of the long bones. From the relative values of HI, LI and HW there must be at least two of these, one (4) affecting specifically the tarsometatarsus, the other (5) affecting the coracoid and scapula. Finally, (6) a factor affecting the length of the nasal region and lower jaw, relative to the cranium. This last might perhaps be regarded as a collateral effect of (2), the beak being regarded as one of the 'extremities' of the body. However, if (2) really represented a factor for elongation of the extremities in general, one would expect to find HI and LI showing a difference of this kind in the wing: as has been seen, they do not.

The statistical significance, in the narrow sense, of all these differences is not in question: that is, they are not due simply to accidents of sampling, but are genuinely characteristic of the different lines. It is perhaps more questionable whether they are all to be regarded as invariable side-effects of the methods of selection practised. It is at least conceivable that a repetition of the selection experiment, using the same selection criteria and either the same or different foundation stocks, might have given different results. This possibility seems most seriously to be reckoned with in the case of the shape factors (4), (5) and (6), which have no obvious relationship to the index used in selection. Had one been asked, on the other hand, to predict the collateral effects of selection for the index, one might very well have suggested differences like (1), (2) and (3); if anything is surprising here, it is that (2) should form so large a portion of the total response, and that (1) should be so small.

Perhaps the most important aspect of the present results is to emphasize how diverse and unexpected some of the collateral effects may be, when one embarks on selection aimed at altering the proportions of the body. As Darwin remarked in *The Origin of Species* (1872, p. 114): '. . . the whole organization is so tied together that, when slight variations in one part occur, and are accumulated through natural selection, other parts become modified. This is a very important subject, most imperfectly understood . . .'

SUMMARY

Comparisons of skeletal dimensions are made between adult females of four lines of fowl, selected respectively for relatively long and short shanks (HI and LI) and for high and low body wieght (HW and LW) at 10 weeks of age. It is shown that elongation of the leg in HI compared with LI is greatest in the tarsometatarsus, least in the femur. HW and LW are intermediate in this respect. There is no comparable proximo-distal gradient of elongation in the wing. HI differs from LI in a manner comparable to ectomorphy in humans: limb bones are all longer in HI but relatively (and in most instances absolutely) thicker in LI. HW is again intermediate in this respect. The nasal region of the skull is disproportionately elongated in HI compared with LI. In certain bones HI and LI differ widely in cross-sectional

shape of the shaft: LI is flatter than HI in the tarsometatarsus, less flat in the coracoid and scapula. HW resembles in each case the line with the less flattened cross-section.

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