

Severe undernutrition in growing and adult animals

9.* The effect of undernutrition and its relief on the mechanical properties of bone

BY R. A. McCANCE AND J. W. T. DICKERSON

*Medical Research Council Department of Experimental Medicine,
University of Cambridge*

AND G. H. BELL AND OLIVE DUNBAR

Department of Physiology, Queen's College, Dundee

WITH AN APPENDIX BY A. GIBB

Department of Civil and Mechanical Engineering, Queen's College, Dundee

(Received 22 February 1961—Revised 14 August 1961)

It is generally accepted that age affects the properties and composition of bone but it is not really clear from the papers of McCay, Crowell & Maynard (1935), McCay, Maynard, Sperling & Barnes (1939), or in the account by McCay (1942) whether the abnormalities in the bones described by them were the result of undernutrition or of old age. Undernutrition in young growing animals has a profound effect upon the structure of the bones (Pratt & McCance, 1960) and alters their chemical composition (Dickerson & McCance, 1961). It has also been found to produce bones which break up easily and splinter during cleaning. A series of bones from undernourished animals has, therefore, been subjected to the procedures described some time ago for studying their breaking stress and elasticity (Bell, Cuthbertson & Orr, 1941; Weir, Bell & Chambers, 1949). The same bones have been analysed for water and ash and the results are reported in this paper.

MATERIALS AND METHODS

The care and feeding of the animals used in this investigation have been described elsewhere (McCance, 1960). The results presented here were obtained from tests made on one femur from each animal listed in the tables. Great care was taken to remove the bones from the carcasses without damaging the periosteal surfaces since slight cuts into the cortical bone may lead to serious underestimates of breaking stress. Some time had to elapse between the death of the animals and the test; this was occupied in removing the bone from the animal, in transport between Cambridge and Dundee, cleaning it and preparing it for experiment. No fixatives or antiseptics were used since these would affect the physical properties of the bone by acting on the collagen. In order to standardize the loss of moisture as much as possible, the bones were left for some time at room temperature, to allow them to come into equilibrium with their surroundings, before they were subjected to test.

* Paper no. 8: *Brit. J. Nutr.* (1961), 15, 567.

Only the principles of the mechanical tests will be given; the details are described in the papers already quoted (Bell *et al.* 1941; Weir *et al.* 1949) and more recently they have been reviewed (Bell, 1956). Hemicylindrical pieces of resin were cast on to the two ends of each bone in a standard position and the bone was laid, as a bridge, across two strong metal supports, one hemicylinder sitting on each support. The distance between the lines of contact between the hemicylinders and the supports is the span (l). A smooth hook placed over the mid-point of the bone was attached to a calibrated spring balance and then to a turn-buckle fixed to the floor. By adjusting the turn-buckle increasing loads (W) were applied and the sag of the mid-point of the bone (y) was read on a dial gauge. Readings of load and sag were made as the load was slowly and steadily increased up to the breaking point.

At the fracture site at the middle of the shaft the cockerel bones were elliptical in section (in fact nearly circular) with a concentric elliptical marrow cavity and the moment of inertia (I) was obtained from the simple formula $I = \frac{1}{64}\pi(BD^3 - bd^3)$, where B and D are the external breadth and depth at the mid-shaft and b and d are the breadth and depth of the marrow cavity at the same place. The breaking stress (S_B) was calculated from the formula $S_B = WD/8I$. Young's modulus was calculated from the slope of the straight line drawn through the simultaneous readings of W and y . The strain at the elastic limit (i.e. the elongation of the undersurface of the bone at the point at which the graph of W against y departed from the straight line) was calculated and is expressed as a percentage.

The calculations of breaking stress and Young's modulus are based on simple theory of bending of beams. We know that there are objections to such a simple treatment which cannot give absolute values, especially since bone is not isotropic. But, for the purposes of this inquiry which are to compare the quality of the material of bones, simple treatment seems to us to be justifiable. A further objection is that the results might be influenced by the rate of loading, but in practice the rate of loading was much the same in all experiments, either because the hydraulic press was adjusted to a certain speed or because the turn-buckle was adjusted by hand and readings were made regularly as the load increased.

Some of the bones from the older pigs were too large and strong to be broken by this simple apparatus. They were tested in an Avery hydraulic press. The bone ends were cemented into rectangular metal boxes in a standard position by means of a mixture of colophonium resin and plaster of Paris. The metal boxes rested on hemicylindrical steel rests and a round rod was applied to the centre of the bone; the weight was increased steadily until the bone broke. The deflexion y was measured by a dial gauge as before.

A certain amount of difficulty arose from the fact that the cross-section of the mid-point of these large bones was too irregular to permit the calculation of moment of inertia by a simple formula. To obtain the external dimensions the bone was set up in a lathe and turned slowly while readings were made on a dial gauge pressing lightly on the middle of the shaft. The dial-gauge readings were plotted on circular graph paper and were checked by reference to a cast in dental stone which had previously been made. When the bone was broken the measurements of cortical thickness were trans-

ferred to the graph and a complete picture of the cross-section of the mid-point of the bone was obtained at a magnification of ten times. The method of calculating the moment of inertia is given in the appendix. The breaking stress was calculated from the formula $S_B = Wlx/4I$, where W is the load, l the span and x the distance from the centroid to the upper or lower surface, whichever was the greater. The calculations of Young's modulus and of the strain at the elastic limit were made as before.

Some idea of the range of measurements can be obtained from the fact that the load necessary to break the smallest chicken bone was only 4.1 kg, whereas the largest of the pig bones supported 470 kg before failure. However, in considering the results it is essential to realize that the three values, breaking stress, Young's modulus and strain at elastic limit are measures of the quality of the bone material and are independent of the actual size of the anatomical bone used. These values may, therefore, be used to make direct comparisons between the physical properties of two bones of quite different shapes and sizes.

Since the mechanical tests assess the physical properties of the cortical bone at the middle of the shaft, the results of these tests must be related to the chemical properties of the bone at the same site. Fragments for analysis were therefore taken from the middle third of the shaft and both the periosteal and endosteal surfaces were cleaned with a dental burr to ensure that the material examined was entirely cortical bone. The superficial area of the fragments was about 1 cm² for the cockerels and about 2 cm² for the much larger pig bones. Since cortical bone only was analysed, the values for ash and water in the tables may be somewhat different from those usually quoted in the literature which have generally been obtained by a study of intact bones or cross-sections. The chemical results presented in this paper are in general agreement with those obtained by Dickerson & McCance (1961) in their more detailed study of the humerus.

RESULTS

Table 1 shows the effect of growth upon the breaking stress, Young's modulus of elasticity, strain at the elastic limit and chemical composition of the femurs of well-nourished cockerels and pigs. It is necessary to have this information in order to

Table 1. *Breaking stress, Young's modulus of elasticity, strain at the elastic limit and the ash-water-volume relationships in the cortex of the mid-shaft of growing bones in well-nourished cockerels and pigs*

(Values are means for the number of animals shown)

Age (weeks)	Cockerels					Pigs		
	2	4	27	34	42	3.4	14	43
No. of animals	12	9	6	2	4	9	4	3
Mean body-weight (kg)	0.1	0.2	3.5	3.7	3.9	5.9	40.4	183
Mean femur weight (g)	0.32	0.66	18.1	17.3	18.5	10.9	113	353
Breaking stress (kg/mm ²)	14.5	14.4	21.6	22.0	22.6	15.3	13.7	14.7
Young's modulus $\times 10^{-3}$ (kg/mm ²)	0.56	0.84	1.13	1.13	1.27	0.34	0.79	1.58
Strain at elastic limit (%)	1.9	1.4	1.7	1.8	1.8	3.67	1.60	0.70
Ash in dehydrated bone (%)	56.3	63.2	63.6	67.2	67.5	60.4	68.3	68.8
Water (%)	12.2	11.6	10.1	10.0	9.6	12.5	11.2	9.8
Ash/unit volume (g/ml)	0.62	0.90	1.06	1.19	1.26	0.84	1.09	1.24

understand the effects of undernutrition because, in the animals undernourished from an early age, maturation proceeded to some extent during the period of undernutrition. In well-nourished cockerels, the breaking stress increased with growth and so did Young's modulus of elasticity; the percentage of ash in the dehydrated bone and also the amount of ash per unit volume increased; the strain at the elastic limit did not alter with age. The percentage of water decreased with increasing age, but too much reliance should not be placed on small differences here since the quantity of water found in the portions of the bone taken for analysis must have varied to some extent with the time which elapsed between the dissection and analysis and with the atmospheric conditions. In well-nourished pigs, there was no change in the breaking stress within the age period studied, but there was an increase in Young's modulus (much larger than in the cockerels) and a considerable decrease in the strain. The changes in the percentage of ash in the dehydrated bone and in the ash per unit volume were in the same direction as in cockerels. In both species the differences between the percentage of ash in the oldest and youngest bone examined were statistically significant ($P < 0.01$ for both species).

Table 2 shows the effect of underfeeding on the bones of growing chickens and pigs. In each species, two comparisons are shown, first between the undernourished animals and well-nourished animals of the same size and second between the undernourished animals and well-nourished animals of the same age.

Table 2. *Effect of underfeeding young cockerels and pigs upon the breaking stress, Young's modulus of elasticity, strain at the elastic limit and the ash-water-volume relationships in the cortex*

(Values are means for the number of animals shown)

	Cockerels			Pigs		
	'Weight' control	Under-nourished	'Age' control	'Weight' control	Under-nourished	'Age' control
Age (weeks)	4	27	27	3.4	28-52	28-52
No. of animals	9	13	6	9	14	3
Body-weight (kg)	0.2	0.2	3.5	5.8	4.7	183
Weight of femur (g)	0.66	0.82	18.1	10.9	11.5	352
Breaking stress (kg/mm ²)	14.4	18.8***	21.6	15.3	14.1	14.7
Young's modulus $\times 10^{-3}$ (kg/mm ²)	0.84	1.62***†††	1.12	0.34	0.65***††	1.57
Strain at elastic limit (%)	1.4	1.0***†††	1.7	3.67	2.04***†††	0.70
Ash in dehydrated bone (%)	63.2	67.2*†††	63.6	60.4	70.2***	68.8
Water (%)	11.6	9.1***†	10.1	12.5	11.0***	9.8
Ash/unit volume (g/ml)	0.90	1.09**	1.06	0.84	1.22***	1.24

Difference between undernourished and 'weight' control statistically significant: *** $P < 0.01$, ** $0.01 < P < 0.02$, * $0.02 < P < 0.05$.

Difference between undernourished and 'age' control statistically significant: ††† $P < 0.01$, †† $0.01 < P < 0.02$, † $0.02 < P < 0.05$.

The bone of the undernourished cockerels had a breaking stress greater than that of healthy birds of the same size and not significantly different from that of animals of the same age. Young's modulus was higher ($P < 0.01$) in the undernourished group than in either of the two groups of control animals and the strain was lower ($P < 0.01$). The percentage of water in the cortex was lower ($P < 0.01$) and of ash in the dehydrated

cortex higher ($0.02 < P < 0.05$) than in bone from well-nourished animals of the same body-weight, or age (for ash $P < 0.01$, and for water $0.02 < P < 0.05$). The amount of ash per unit volume was larger ($0.01 < P < 0.02$) than in the younger bone and almost the same as in bone of the same chronological age.

The bones of the undernourished pigs had the same breaking stress as those of younger animals of the same size, but it is to be recalled that maturation did not affect this measurement in pigs. A comparison of the undernourished bones, however, with those of well-nourished animals of the same size shows that in all other respects the changes were similar to those in cockerels, namely, a rise in Young's modulus, in the percentage of ash and in the ash per unit volume and a fall in the strain and the percentage of water. In most respects the values were between those for animals of the same size and those for animals of the same age.

Table 3. *Effect of underfeeding cockerels approaching complete development on the breaking stress, Young's modulus of elasticity, strain at the elastic limit and the ash-water-volume relationships in the cortex*

(Values are means for the number of animals shown)

	Before undernutrition	Undernourished	'Age' control
Age (weeks)	27	42	42
No. of birds	6	8	4
Mean body-weight (kg)	3.5	2.1	3.9
Mean femur weight (g)	18.1	12.0	18.5
Breaking stress (kg/mm ²)	21.6	22.8	26.5
Young's modulus $\times 10^{-3}$ (kg/mm ²)	1.13	1.16	1.27
Strain at elastic limit (%)	1.7	1.8	1.8
Ash in dehydrated bone (%)	63.6	68.9*	67.5
Water (%)	10.1	10.8	9.6
Ash/unit volume (g/ml)	1.06	1.18	1.26

* Difference before and after undernutrition statistically significant ($P < 0.01$).

Table 3 shows that undernutrition in cockerels which had been reared on a full diet until they were 27 weeks old, produced no significant difference in the physical properties of the cortex of the femur. The normal increase in the percentage of ash in the dehydrated bone did, however, take place ($P < 0.01$).

When animals whose growth had been held up were allowed free access to food, they rapidly gained weight and their bones grew. Table 4 shows the effect of rehabilitation on the properties of the bone of the two species.

In cockerels, the first 15 weeks of rehabilitation reduced ($0.02 < P < 0.05$) the mean breaking stress a little, lowered Young's modulus, but increased ($P < 0.01$) strain to a value not significantly different from that of control bone of the same age. It lowered ($0.02 < P < 0.05$) the percentage of ash in the dehydrated bone but made no significant difference to the percentage of water or the amount of ash per unit volume. The changes in breaking stress and Young's modulus tended to make the bone immature compared with its 'age' control, and thus reversed the effects of undernutrition. In the next 12 weeks of rehabilitation the processes of ageing were more in evidence than those just described, and the properties and composition of the bones changed back again

towards those proper to the age of the birds. The breaking stress and the percentage of ash in the dehydrated bone were, however, not yet normal (for the difference in both measurements, $0.02 < P < 0.05$) even for an age of 42 weeks. The differences might have been shown more clearly had control birds 53 weeks old been available for comparison.

Table 4. *Effect of rehabilitating undernourished cockerels and pigs on the breaking stress, Young's modulus of elasticity, strain at the elastic limit and the ash-water-volume relationships in the cortex*

(Values are means for the number of animals shown; values for rehabilitated animals are in bold-face type)

	Cockerels				Pigs		
	Before rehabilitation	Rehabilitated for 15 weeks	Control	Rehabilitated for 27 weeks	Before rehabilitation	Rehabilitated for average of 26 weeks	Control
Age (weeks)	27	42	42	53	36	76	22
No. of animals	13	7	4	4	14	7	6
Mean body-weight (kg)	0.2	2.1	3.9	2.9	4.7	83	83
Mean femur weight (g)	0.82	9.2	18.5	15.5	11.5	186	180
Breaking stress (kg/mm ²)	18.8	16.0*††	26.6	20.7†	14.1	9.2***††	14.1
Young's modulus × 10 ⁻³ (kg/mm ²)	1.62	0.84***††	1.27	1.13	0.63	0.91*	1.02
Strain at elastic limit (%)	1.0	1.6**	1.8	1.65	2.04	0.91**	1.30
Ash in dehydrated bone (%)	67.2	61.6*†	67.5	64.6†	70.2	68.1	68.3
Water (%)	9.1	10.0	9.6	9.1	11.0	9.7	10.9
Ash/unit volume (g/ml)	1.09	1.03	1.26	1.09	1.22	1.14	1.14

Difference between means before and after rehabilitation statistically significant: ** $P < 0.01$, * $0.02 < P < 0.05$.

Difference between means for control and rehabilitated animals statistically significant: †† $P < 0.01$, † $0.02 < P < 0.05$.

Only seven rehabilitated pigs were examined and they had been rehabilitated for various lengths of time. Consequently the weight controls were necessarily of various ages. The breaking stress was reduced ($P < 0.01$) with reference both to a group of undernourished pigs and to the well-nourished 'weight' controls. This change was much less conspicuous in the birds. The mean for Young's modulus rose ($0.02 < P < 0.05$) and the seven individual pigs showed a steady increase with the progress of rehabilitation. The change in Young's modulus with age has been seen to be considerable in pigs (Table 1). In the rehabilitated animals it was not as high as in the oldest group of normal animals (Table 1) and was almost the same as in the 'weight' controls. The strain was reduced ($P < 0.01$) during rehabilitation to a value not significantly different from that of the 'weight' controls. There was no significant change during rehabilitation in the chemical properties of the bone.

Table 5 summarizes the main findings presented in Tables 1, 2 and 4.

Table 5. *Effect of growth, undernutrition and rehabilitation of pigs and cockerels on the mechanical properties and composition of the cortex*

(Summary of findings shown in Tables 1, 2 and 4)

	Growth		Undernutrition*		Rehabilitation†	
	Pigs	Cockerels	Pigs	Cockerels	Pigs	Cockerels
Breaking stress	Unchanged	Increased	Unchanged	Increased	Decreased	Decreased initially, but gradually returned to normal
Young's modulus	Greatly increased	Slightly increased	Increased, but less than normal for age	Increased, more than normal for age	Increased to nearly normal for weight	Decreased initially, but gradually returned to normal
Strain at elastic limit	Greatly decreased	Almost unchanged	Decreased, but less than normal for age	Decreased	Decreased beyond normal for weight	Increased to normal
Percentage of ash in dehydrated bone	Increased	Increased	Increased, almost normal for age	Increased, higher than normal for age	Decreased a little to normal for weight	Decreased initially, but tended to return to normal
Ash/unit volume	Increased	Increased	Increased, normal for age	Increased, normal for age	Decreased a little to normal for weight	Not significantly changed

* Unless otherwise stated, the change is relative to bone structure of animal of similar weight but not undernourished.

† Change relative to values before rehabilitation.

DISCUSSION

The application of these engineering concepts to biological material calls for some explanation and rather careful interpretation. In these experiments the load bends the bone so that the surface of the shaft uppermost in the testing machine is concave and is in compression; the undersurface is in tension, i.e. is being elongated, and fails when the tension exceeds the value known as the breaking stress. This measurement increased in cockerels as they got older and undernutrition did not prevent this. Rehabilitation at first lowered the breaking stress, but it increased again as the period of rehabilitation was prolonged. Neither age nor undernutrition affected this measurement in pigs but it was considerably reduced by rehabilitation.

Young's modulus is the relationship between tensile stress and strain within the range in which the bony material obeys Hooke's law; in other words, it is the slope of the straight portion of the stress-strain curve. Young's modulus is most easily thought of as an index of stiffness; the higher the value the stiffer is the material. Like breaking stress it describes the quality of the material and is independent of the size since it also is expressed in kg/mm^2 . Age increased Young's modulus slightly in cockerels and greatly in pigs. Undernutrition did not prevent this change and rehabilitation reversed it in the cockerels though not in the pigs, that is in the cockerels it reduced the

true elasticity of the bone and produced a sign of immaturity in bone which was chronologically ageing.

The word strain is used in this paper to indicate the elongation of the convex under-surface of the bone, expressed per 100 units of length, when it is under tension up to its elastic limit. The elastic limit is taken as the point at which the deflexion ceases to be proportional to the load. (For further explanation see Weir *et al.* (1949), and especially Fig. IV in that paper.) A recent examination of rat tail tendon (Rigby, Hirai, Spikes & Eyring, 1959) shows that the strain at the elastic limit is of the order of 4%, and it may be that, in bone, strain at the elastic limit expresses a property of the collagen in it. Age made little difference to this measurement in cockerels but under-nutrition reduced it, and the change was reversed by rehabilitation. Age greatly reduced strain at the elastic limit in pigs. Undernutrition delayed this change, but it is difficult to separate the effects of age from those of rehabilitation for they appear to have been the same.

The physical properties of bone are a measure of the quality of the material in the cortex and this must depend upon its structure and chemical composition. Bone is, however, not homogeneous, so that any attempt at a correlation of these aspects of bone with its mechanical properties must, to a certain degree, be of a tentative nature.

Pratt (1961) has described the changes in the structure of the fowl femur during growth. It is possible, on the basis of Pratt's work, to suggest that two factors may be responsible for the increase in the breaking stress of the cortex of the fowl femur with age. These factors are (1) the incorporation into the cortex of elastic fibres, and (2) the surface deposition of lictor-bundle bone, i.e. bone in which the matrix is formed of longitudinally arranged and densely packed fibre bundles (Weidenreich, 1930). A considerable number of elastic fibres have appeared in the fowl cortex by 17 weeks. Bones from cockerels killed before and after this age, that is at 15 and 18½ weeks, showed, however, no change in the breaking stress. Lictor-bundle bone begins to appear at the same time as the elastic fibres, and continues to appear in considerable amounts while there is little increase in the number of elastic fibres, so that in a bone of a year-old cockerel it probably forms up to 75% of the cortex. This lictor-bundle bone is densely fibred and the fibres are orientated in the long axis of the bone. It is suggested that it is the deposition of lictor-bundle bone, rather than that of elastic fibres, that is responsible for the increase of the breaking stress of the fowl femur after 18½ weeks of age. Lictor-bundle bone has not been found in the cortex of the pig femur up to an age of 11 months and no increase in the breaking stress has been found up to this age, and thus the difference between the two species could be accounted for on this basis.

The breaking stress of the cortical bone of cockerels undernourished for 25 weeks was higher than it was at the beginning of undernutrition, but it had not increased to the level found in the cortex of well-nourished birds of the same age. There are no elastic fibres within the matrix of the undernourished bones. Undernourished avian bone is, in fact, different structurally from that of well-nourished animals of any age, for it is very finely and densely fibred (Pratt & McCance, 1960). It does, however, resemble to some extent the bone of well-nourished adult cockerels in that there is a

wide subperiosteal zone with a compact structure. Here again the fibres are very dense and arranged in a predominantly longitudinal direction though they are not as coarsely bundled and evenly arranged as in the lictor bundles.

There was no change in the breaking stress of the cortical bone of the pig's femur during undernutrition. Two reasons for the difference between the two species may be suggested. First, there is a difference between the fowl and the pig in the way undernutrition modifies the structure of the femur. In the undernourished cockerels all the cortex present when underfeeding began was resorbed during the period of undernutrition. In the undernourished pigs it was not so, and a large proportion of the wall of the shaft of the femur consisted of the original bone, and on the subperiosteal surface of this bone there had been some deposition of compact densely fibred bone. It would seem, however, that this kind of bone formed a smaller proportion of the wall of the shaft in the pig than in the cockerel (Pratt, personal communication). Secondly, X-ray photographs of the pig's femur suggest (Pratt, personal communication) that undernutrition in this species may produce changes in the angle of torsion (i.e. the angle formed by the axis of the head and neck projected upon that of the condyles) and these changes may tend to reduce the breaking stress in spite of the subperiosteal compact tissue. Thus, the value of the breaking stress shown in the tables may be lower than it would have been if the bone had been normal in shape. Changes in the angle of torsion would be unlikely to occur in the fowl femur where there are no secondary centres of ossification. During the rehabilitation of undernourished pigs it is probable that this change in the angle of torsion persists, and thus the breaking stress of the bone is reduced.

The values for the breaking stress of the bone of the cockerels killed at 15 weeks of age, for the elucidation of the influence of elastic fibres, were similar to those of the bone of cockerels rehabilitated for 15 weeks. The bone of the cockerels rehabilitated for a further 12 weeks (a total of 27 weeks' rehabilitation) possessed properties similar to those of the bones of normal birds aged 27 weeks. The mechanical properties of the bone of the rehabilitated cockerels were, therefore, not those of their chronological age, but of bone which had been growing only for the chronological period of rehabilitation. With the exception of the breaking stress, this generalization applied also to the pigs. Pratt & McCance (1961) found that the structure of the bone of undernourished birds rehabilitated for 11-11½ weeks was similar to that in well-nourished normal birds of 10 weeks of age.

Weir *et al.* (1949) suggested that the low breaking stress of rachitic bone was due to its decreased mineralization, but they were not able to show conclusively that the low percentage of ash in the bones was the only factor. In the light of the results of the experiments described here and in the above discussion it is possible that the reduction in breaking stress of rachitic bone may be, at least in part, due to the atypical nature of its organic matrix (Engfeldt & Hjertquist, 1960). On the basis of their experiments with rachitic bone Weir *et al.* (1949) suggested that the strain at the limit of elasticity may depend on the physical properties of the collagen and not on its degree of mineralization. If it is so, the changes must take place with increasing age in normal pigs but not in normal cockerels, and the small reduction in strain at the elastic limit in the

undernourished pigs can be explained by the 'mixed' structure of the bone, and by supposing that the collagen laid down during underfeeding failed at a smaller extension than the collagen formed when the animal was well nourished.

SUMMARY

1. The effects of growth, undernutrition and subsequent rehabilitation on the mechanical properties of cortical bone have been studied in pigs and cockerels.
2. During normal growth the breaking stress increased in cockerels, but not in pigs; the percentage strain at the elastic limit decreased in pigs but did not change in cockerels; there was a greater increase in Young's modulus of elasticity in pigs than in cockerels; in both species the percentage of ash in the dehydrated bone, and the amount of ash per unit volume, increased.
3. Undernutrition did not prevent some increase with age in the breaking stress in cockerels but caused no change in this property in the pigs. In both species there was a rise in Young's modulus, in the percentage of ash and in the amount of ash per unit volume and a fall in the percentage strain at the elastic limit and in the percentage of water.
4. Rehabilitation of the undernourished animals caused most of the properties of their bones to revert to those characteristic of much younger animals. The major exception to this generalization was the large fall in breaking stress of the bone of rehabilitated pigs.
5. The mechanical properties of the cortex are discussed in relation to its structure and chemical composition.

The authors desire to thank Messrs Stan and Terry Cowan for their care of the animals, Mrs Jean Oliver for making some of the measurements on the bones, and Miss C. M. Popplewell of the Computing Machine Laboratory, University of Manchester, for considerable help with the calculations. This work was supported by grants from the Medical Research Council.

APPENDIX

A method of finding the moment of inertia of an irregular section with transparent templates

The moment of inertia I_{xx} of any section, such as is shown in Fig. 1, about its centroid is $I_{xx} = \int y^2 dA = \int by^3 dy$, where y is the distance of an element of area dA from the centroid of the section. More simply, it may be stated that the moment of inertia varies as the breadth of the section and as the cube of its depth, and that an element of area makes a greater or smaller contribution to the moment of inertia according as whether it is more or less distant from the centroid. For example, the moment of inertia of a rectangle of breadth B and depth D is $\frac{1}{2}BD^3$. In Fig. 2 is shown a series of rectangles, all having the same breadth, whose moments of inertia are in the ratio 1:2:3:4. The depths of these rectangles are in the ratio

$$3\sqrt{1}:3\sqrt{2}:3\sqrt{3}:3\sqrt{4}.$$

This suggests the use of a template method for finding the moment of inertia of an irregular section, by measuring the intercepts made by the outline of the section on a series of template lines. The semi-depth of a rectangle of unit breadth 1 in., and moment of inertia equal to 2 in⁴, is $3\sqrt{3}$ in. Thus the spacing of template lines to indicate rectangles of unit breadth and moments of inertia of 2, 4, 6, 8 in⁴ will be at $3\sqrt{3}$, $3\sqrt{6}$, $3\sqrt{9}$, $3\sqrt{12}$ in., etc. (namely 1.442, 1.817, 2.080, 2.289 in., etc.) from a datum line, the lines being plotted on each side of the datum line.

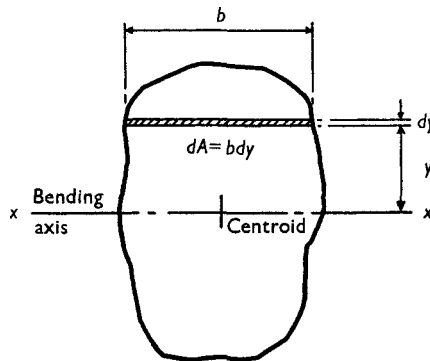


Fig. 1. Terms used in finding the moment of inertia of a section.

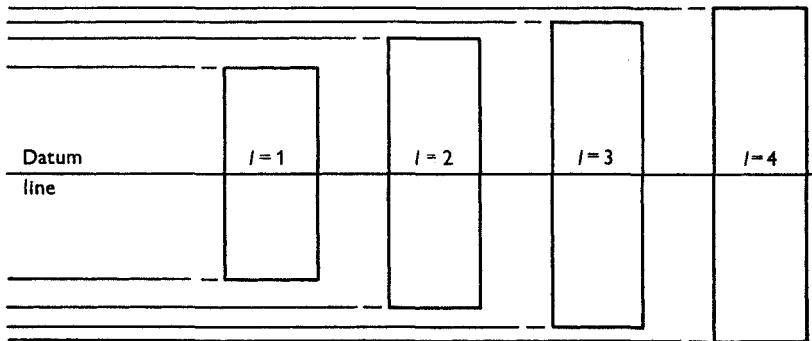


Fig. 2. Relative depths of rectangles whose moments of inertia are in the ratio 1:2:3:4.

The part of a section cut off by two successive template lines approximates to a trapezium, and the mean of the intercepts on these two lines is taken to represent the contribution made by that part towards the total moment of inertia. This assumes that the moment of inertia of the trapezium is the same as that of a rectangle having the same area between the same two template lines—which is true with very little error. The method of using the template is, therefore, to place it over the section, as shown in Fig. 3, so that the datum line lies on the bending axis. The lengths of all intercepts made by the section boundaries on the template lines including the datum line are measured. The moment of inertia is the sum of the intermediate intercepts plus half the sum of the top and bottom intercepts.

If the line spacings quoted above are used the moment of inertia is given directly in in⁴. If the total depth of the cross-section being investigated is much smaller or much larger than 9 in. a closer or wider line spacing can be used with a suitable correction factor.

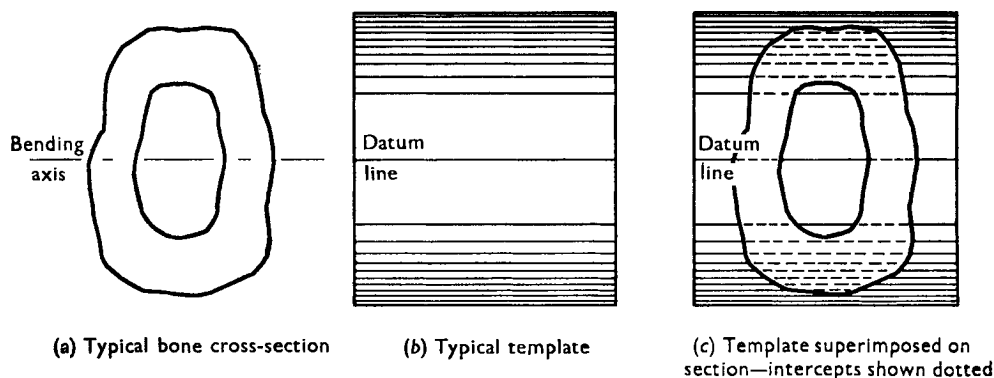


Fig. 3. Method of using the template on a typical cross-section.

To gain experience in the use of the template it is useful to check the results obtained on a standard section. A useful section is a circle of diameter 7 in. which has $I_{xx} = 118 \text{ in}^4$. In such a trial with a template with a scale correction factor of 1.125, a value of 118.4 in^4 was obtained—an error of less than 0.5%.

REFERENCES

- Bell, G. H. (1956). In *The Biochemistry and Physiology of Bone*, Chapter 2. [G. H. Bourne, editor.] New York: Academic Press Inc.
- Bell, G. H., Cuthbertson, D. P. & Orr, J. (1941). *J. Physiol.* **100**, 299.
- Dickerson, J. W. T. & McCance, R. A. (1961). *Brit. J. Nutr.* **15**, 567.
- Engfeldt, B. & Hjertquist, S. O. (1960). In *World Review of Nutrition and Dietetics*, Chapter 8. [G. H. Bourne, editor.] London: Pitman Medical Publishing Co. Ltd.
- McCance, R. A. (1960). *Brit. J. Nutr.* **14**, 59.
- McCay, C. M. (1942). In *Problems of Ageing*, Chapter 26, 2nd ed. [E. V. Cowdry, editor.] Baltimore: Williams and Wilkins.
- McCay, C. M., Crowell, M. F. & Maynard, L. A. (1935). *J. Nutr.* **10**, 63.
- McCay, C. M., Maynard, L. A., Sperling, G. & Barnes, L. LeR. (1939). *J. Nutr.* **18**, 1.
- Pratt, C. W. M. (1961). *J. Anat., Lond.*, **95**, 110.
- Pratt, C. W. M. & McCance, R. A. (1960). *Brit. J. Nutr.* **14**, 75.
- Pratt, C. W. M. & McCance, R. A. (1961). *Brit. J. Nutr.* **15**, 121.
- Rigby, B. J., Hirai, N., Spikes, J. D. & Eyring, H. (1959). *J. gen. Physiol.* **43**, 265.
- Weidenreich, F. (1930). *Das Knochengewebe*. In *Handbuch der mikroskopischen Anatomie des Menschen*, p. 416. [W. von Mollendorff, editor.] Teil 2. Berlin: Julius Springer.
- Weir, J. B. de V., Bell, G. H. & Chambers, J. W. (1949). *J. Bone Jt. Surg.* **31B**, 444.