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Mechanical properties of very young bone in the axis deer (*Axis axis*) and humans

J. D. CURREY
Department of Biology, University of York, York YO1 5DD

AND CAROLINE M. POND
Department of Biology, The Open University, Milton Keynes MK7 6AA

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(With 2 figures in the text)

The mechanical properties of bone from a pregnant axis deer, her full-term foetus, three young children, and an adult man, were compared. The properties of the bone of the foetal deer were more similar to those of the man than to those of the children, and corresponded to the high degree of mineralization of the foetal bone. These properties accord with the different habits and selective pressures acting on children, and on neonatal deer.

Contents

Introduction

There is good evidence that many of the differences in the mechanical properties of adult bone are adaptive (Currey, 1979*a*).

Several studies have showed well-marked changes in mechanical properties of bone during ontogeny (Currey & Butler, 1975; McPherson & Kriewall, 1980; Kriewall, McPherson & Tsai, 1981; Torzilli *et al.*, 1981*a*, *b*). Currey (1979*b*) argued that the relatively high impact resistance of the bones of young humans, and the relatively high Young's modulus of mature human bone, could be interpreted as adaptations to changes in habits during ontogeny. He argued that stiffness is important for efficient locomotion, but that the clumsy and exploratory phase of human life would be better served by bones that, although not as stiff as those of the adult, were more forgiving of falls, in that they were able to absorb more energy without failure. In humans, the changes in the mechanical properties are produced by changes in the degree of mineralization, and there is good evidence of similar situations in many other vertebrates (Currey 1987, 1988).

A counter-argument would be that these age-related differences are not adaptive, but merely represent stages of development; the bone in young humans has not matured and has not had time to achieve the degree of mineralization necessary to achieve a high stiffness.

A natural experiment to resolve this argument would be to examine the bone of a terrestrial

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mammal for which efficient locomotion soon after birth is essential for survival. An example is large ungulates, which are well known for their ability to stand soon after birth, and to follow the herd shortly thereafter. Such animals would be expected to have relatively stiff bone. Although they are ungulates, domestic livestock such as cattle and sheep have been selected for high fecundity, rapid growth and precocious maturity, which make them slightly inappropriate as the subjects of a good natural experiment. This paper reports mechanical and other tests on young children and an adult human, and similar tests on a foetal axis deer *Axis axis* and its mother. The axis deer is not quite such a good natural experimental animal as, for example, a wildebeest. The new-born of the latter species stays with the herd from birth, but the axis deer 'remains hidden in dense cover, with the mother feeding nearby, until it has sufficient strength to roam with the herd' (Novak & Paradiso, 1983). In comparison, the human baby can barely walk at one year old, and the mother carries it in emergencies till a much greater age, so the baby's skeleton is not subjected to very large loads until it is much older.

Materials and methods

The human material came from the femora of 4 individuals: a 35-year-old man, and 3 children aged 5, 5 and 3. None had died of causes likely to have produced effects on the bones, and none had been bedridden before death. The deer material came from the femora of a female aged 2 years and 7 months, and her foetus. The female weighed 53 kg, of which 5% was dissectible adipose tissue, which indicates that she was in good condition. She was born and raised in captivity at Whipsnade Park Zoo, but had not been selectively bred. She was destroyed after she fractured her humerus and the phalanges of a hind leg. The female foetus was judged at autopsy to be nearly full-term, and weighed 4·2 kg.

Specimens from the femora were machined to a uniform size and tested, wet, in tension at room temperature. The method is as described in Currey (1988). Briefly, the tensile specimens had a gauge length of 10 mm, and a cross-section of about 2 mm by 1·5 mm. The specimens were loaded with the head of the testing machine travelling at 200 mm per minute, which produces a strain rate of about 0·2 s^{-1}. Extension was measured by an extensometer. The load was measured by the load cell of the tensile testing machine. The load-deformation curve was displayed on the screen of a storage oscilloscope, and data reduced from a photograph taken of the screen (this included converting the load-deformation curve to a stress-strain curve, which has the same shape, but different units). Various mechanical properties were calculated, of which the following are reported here: Young's modulus of elasticity, ultimate stress, ultimate strain, the resilience, that is the work done on unit volume of the specimen up to the yield point, as measured from the stress-strain curve, and the total work per unit volume absorbed by the specimen up to fracture. The yield point was taken to be where the stress-strain curve deviated by a strain of 0·002 from the initially straight part of the curve. All the specimens had essentially the same dimensions, so work done per unit volume is not confounded by size effects.

A small block of bone was taken just behind one fracture surface, and the calcium content per unit dry weight of bone determined by a colorimetric method (Sarkhar & Chauhan, 1967). An undecalcified cross-section, and a longitudinal section (arranged so that it was a radial longitudinal section with reference to the femur from which it came) were taken from just behind the other fracture surface. The porosity of the cross-section was determined by a point counting method, and an estimate made of the general orientation of the bone with respect to the direction of loading. (It should be said that this varied little in these specimens, and was of no help in explaining the mechanical results.) Observations were made of the histology of the bone as seen in these sections.

Results

The principal results are shown in Table I. (In what follows we state whether the means for particular values are higher or lower than others, usually without referring to the level of

TABLE I

Mean values of the properties of the six femora tested

Bone	E	$\varepsilon_{\mathrm{ult}}$	σ_{ult}	Work (total)	Work (elastic)	Work (plastic)	Calcium	Porosity	N
Human:									
3-year-old	7·0**	0·053*	123	42·5**	2·2	40·3**	222*	8·4*	4
5-year-old	10·4	0·042*	136	37·8	3·7	34·1	225	6·3**	4
5-year-old	12·6	0·044	156*	46·2**	3·2	43·0*	230	4·9**	3
35-yr-old	16·7*	0·029	166**	27·5	2·8	24·7	249	8·3	4
Axis deer:									
Foetus	13·2	0·029	124	19·1	3·5	15·6	242	15·2	4
Mother	31·6**	0·019**	221**	10·0*	1·8*	8·2	274*	3·4**	3

E: Young's modulus of elasticity (GPa)
$\varepsilon_{\mathrm{ult}}$: Ultimate strain
σ_{ult}: Ultimate stress (MPa)
Work: Work under the stress/strain curve (MJ m^{-3})
Calcium: Calcium content of bone (mg/g dry bone)
Porosity: Porosity (%)
N: Sample size

The asterisks represent levels of significance of differences of the means, as measured by *t*-tests, with respect to the axis deer foetus. * $P<0{\cdot}05$; ** $P<0{\cdot}005$

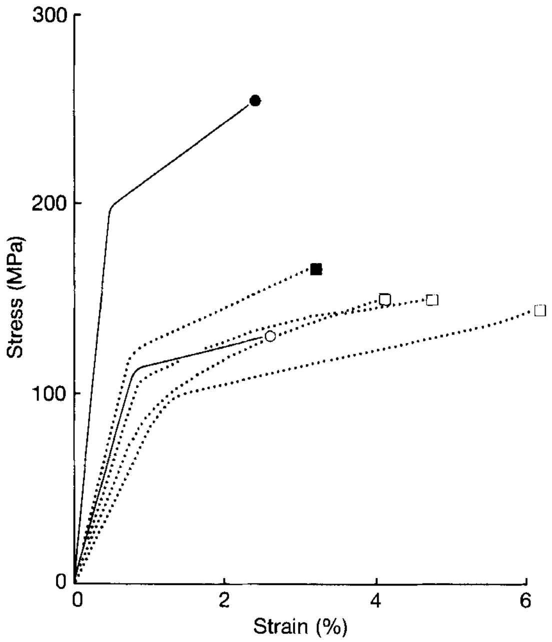
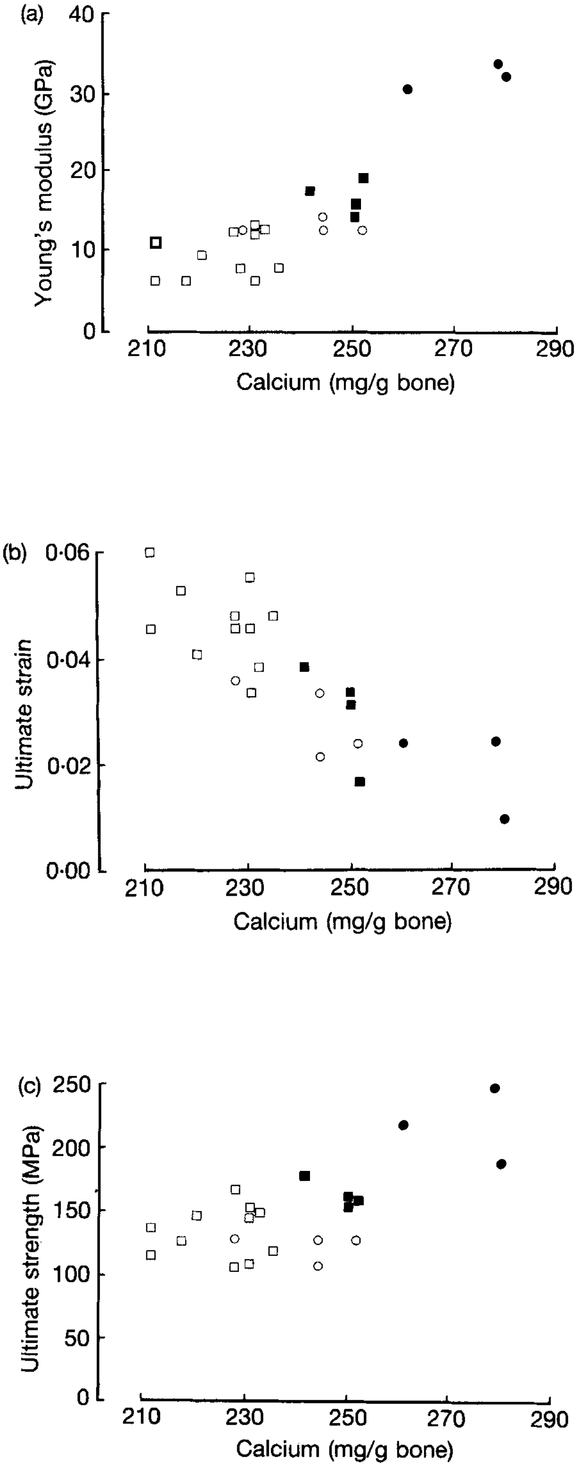


FIG. 1. Stress-strain curves for one specimen from each bone. Symbols: □, children; ■, 35-year-old adult; ○, foetal deer; ●, mother deer.


(a)
Young's modulus (GPa)
40
30
20
10
0
210
230
250
270
290
Calcium (mg/g bone)
(b)
Ultimate strain
0·06
0·04
0·02
0·00
210
230
250
270
290
Calcium (mg/g bone)
(c)
Ultimate strength (MPa)
250
200
150
100
50
0
210
230
250
270
290
Calcium (mg/g bone)

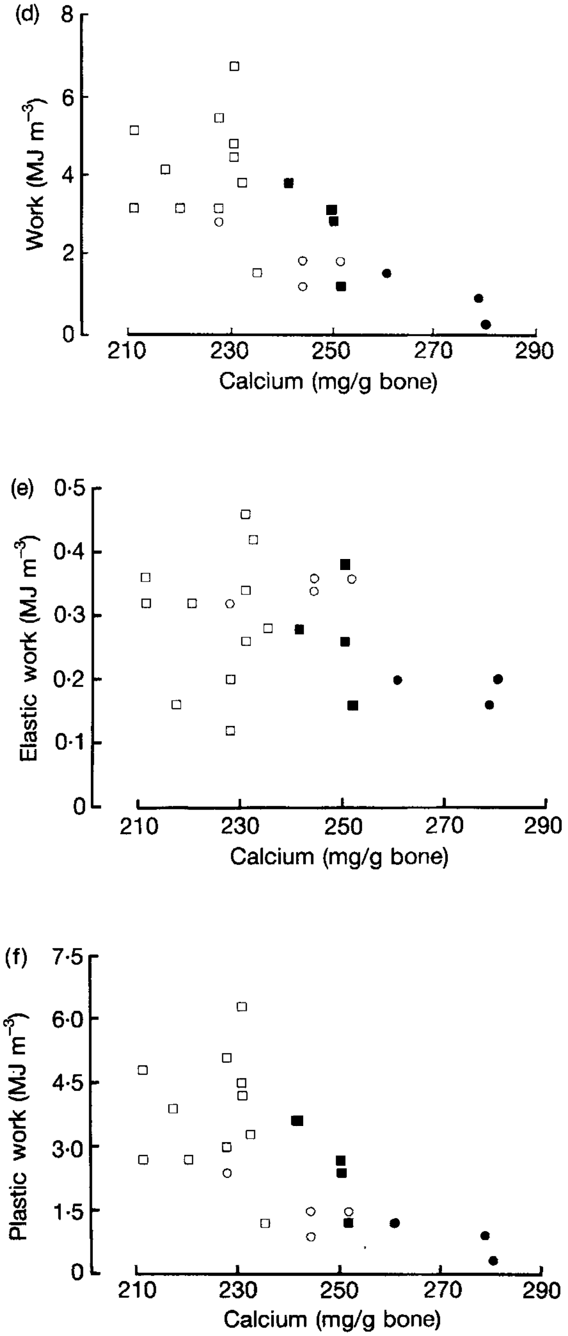


FIG. 2. Relation between calcium content and Young's modulus. Abscissa: calcium content of the dried defatted specimens, in mg/g bone. Ordinate: (a) Young's modulus of elasticity, in GPa; (b) ultimate tensile strain; (c) ultimate tensile strength, in MPa; (d) total work under the stress-strain curve to fracture, in MJ m^{-3}; (e) work under the elastic part of the curve, resilience; (f) work under the plastic, or post-yield, part of the curve. Symbols as in Fig. 1 legend.

TABLE II

Regression equations relating the mechanical variables to the mechanical variables to the two explanatory variables: calcium content and porosity. Power law equations are used, as there is good evidence that these are more appropriate for the present variables than linear equations (Currey, 1987). The linear equations give values, similar to those given by the power law equations, for the significant of the two explanatory variables, although the coefficients are, of course, quite different. R^2 is adjusted for the degrees of freedom. The variables are included in the equation only when they increase the adjusted value of R^2. The subjectively measured value of the orientation of the bone fabric never increased the explanatory power of the equations

Young's modulus	$\propto$	Calcium$^{4{\cdot}9}$ ×	Porosity$^{-0{\cdot}14}$	
		$t=6{\cdot}85$	1·31	$R^2=72\%$
Ultimate strain	$\propto$	Calcium$^{-5{\cdot}1}$ ×	Porosity$^{-0{\cdot}17}$	
		$t=7{\cdot}25$	1·70	$R^2=71\%$
Ultimate stress	$\propto$	Calcium$^{3{\cdot}6}$ ×	Porosity$^{-0{\cdot}23}$	
		$t=3{\cdot}63$	4·06	$R^2=64\%$
Work to fracture	$\propto$	Calcium$^{-6{\cdot}5}$		
		$t=5{\cdot}38$		$R^2=57\%$
Elastic work	$\propto$	Calcium$^{-1{\cdot}3}$		
		$t=1{\cdot}30$		NS
Plastic work	$\propto$	Calcium$^{-7{\cdot}5}$		
		$t=5{\cdot}25$		$R^2=56\%$

significance, if any. The values are given in the table. Of course, it should be borne in mind that 35 more or less independent *t*-tests have been performed, so one would expect about two differences to be apparently significant at the 0·05 level, even if the foetal bone were not different from the others.) Figure 1 shows the load-deformation curve for one specimen from each of the bones, drawn to the same scale. The curve shown is that from the specimen that had a total work under the curve nearest to the mean for that bone.

The foetal deer femur has a mean *Young's modulus* of 13·2 GPa, which is higher than that of any of the three children, and indeed is nearly double that of the three-year-old child. The *ultimate strain* is less than that of the children, and is the same as that of the adult. The *tensile strength* of the deer foetus is the same as that of the three-year-old, and less than that of the older children. The total *work* done in breaking deer foetal specimens is lower than that for any of the human bones. However, the work in the elastic region is not different from any of the human material; the differences in total work result from the work that can be absorbed in the plastic region. The *calcium content* of the deer foetal bone is very nearly as high as that of the adult human. The foetal *porosity* is by far the greatest of any of the bones examined. Surprisingly, the adult human femur had a greater porosity than some of the children's bone.

The axis mother had properties that stand out from the rest, with a very high Young's modulus, a low ultimate strain, a high ultimate stress, and a low value for work done in breaking the specimen. The work is low in both the elastic and plastic parts of the curve. The calcium content is high, and the porosity low. Where comparisons can be made, these results are similar to those from specimens of a fallow deer *Dama dama* tibia, reported by Currey (1987).

The general shape of the stress-strain curves, exemplified in Fig. 1, shows that there is usually a reasonably clearly defined yield region, and that most of the work done on the specimen occurs after yield. The young human bones show much more post-yield strain than the deer bones.

Multiple regression analysis shows that most of the differences between the mechanical properties of the different bones can be explained simply by the differences in their calcium content and porosity (Fig. 2 (a–f); Table II). In general, a higher calcium content is associated with a higher Young's modulus, a higher tensile strength, a lower ultimate strain, and a lower ability to absorb work in the plastic region. Only at the highest values for calcium is the resilience reduced. Porosity has a small negative effect on Young's modulus and ultimate strain, and an important negative effect on ultimate strength.

The high porosity of the deer foetal bone is caused by the fact that it was growing rapidly in diameter, and therefore showed the characteristic appearance of growing fibrolamellar bone, with stacked sheets of parallel-fibred bone being progressively united by lamellar bone. In the three- and five-year-old human bones, the phase of rapid growth had ended and they were not, therefore, very porous. The adult human bone was rather porous, for an adult, due to an unusually large amount of Haversian remodelling. The bone of the adult deer was histologically quiescent, and not very porous.

Discussion

There seem to be no data on the Young's modulus of the long bones of new-born babies. However, McPherson & Kriewall (1980) report a Young's modulus in bending of the cranial bones of about 4 GPa. There are difficulties in extrapolating these results to what might be the case for long bones. However, since a three-year-old child had a femur, which is histologically much more mature than the femur of a neonate, with a Young's modulus of 7 GPa, it is reasonable to suppose that long bones of new-born humans have a Young's modulus that is not greater than about 4 GPa. Torzilli *et al.* (1981*a*), working on new-born dogs, found values of Young's modulus of about 0·5 GPa for the tibia, and 0·8 GPa for the femur. Therefore, almost certainly, the full-term foetus of the axis deer has long bones with a much higher Young's modulus than the human full-term foetus, and a very much higher value than that of the new-born dog which, like the human, is sedentary for some time after birth. The axis foetus has, indeed, a higher Young's modulus than that of a human three-year-old. This relatively high Young's modulus is associated with a relatively high calcium content, and has associated with it the penalties associated with a high mineral content: a low ultimate strain, and a low work to fracture.

In these respects, therefore, the deer foetus serves well as a natural experiment; that is to say, in humans where high stiffness is not important, the bones can remain less mineralized, and tougher, for some years. The new-born deer has to run with the herd soon after birth, and at birth its bones are relatively highly mineralized, stiff, and not very tough. The gestation period for the axis deer is about 8–8½ months, slightly less than that of humans, although the neonate is relatively larger compared with its mother. It is not simply a matter of insufficient time available that makes the young children's bones less highly calcified. Indeed, the histological appearance of the bones of the deer foetus, showing very actively growing fibrolamellar bone, suggests that the calcification of this bone must proceed very rapidly, since its calcium content is almost the same as that of an adult human. The histological appearance of the bone is similar to that figured in Torzilli *et al.* (1981*b*) as characteristic of dog's bone of about six weeks after birth, by which time its Young's modulus had increased little from the Young's modulus at birth. The high porosity of the foetal bone may be responsible for its relatively low strength. No doubt, if it were less porous (a condition required by its high growth rate) it would also have a higher Young's modulus. In the wild, axis deer graze on well-leached tropical soils, eating herbs and grass and sometimes fallen fruit. Such a diet is low in calcium, and the species may be adapted to maximize the efficiency of the sequestration of calcium from the diet.

Torzilli *et al.* (1981*a*, *b*) showed that dog's bone has a very low Young's modulus at birth, but achieves values characteristic of the adult by about 40 weeks of age. This again is what one would expect, because locomotory efficiency is not important for nidicolous animals such as canids. However, in calendar terms, dogs grow to maturity, from a lower birth weight compared with the adult weight, much more quickly than humans. The slight difficulty with this second natural experiment is that dogs are domestic animals, the gross form and possibly also the mechanical properties of whose musculoskeletal system have been modified by artificial selection.

The foetal deer bone has, by virtue of its high calcium content, a limited ability to absorb energy in the plastic region, that is when damage has already occurred. However, it has a resilience, an ability to absorb energy before damage occurs, which is as great as in the human specimens. As Table I shows, the energy absorbed in the elastic region is much less than absorbed in the plastic region.

The final feature to note in the axis deer is how extreme the properties of the adult bone are. It has a very high Young's modulus, a very high tensile strength, a low ability to absorb energy in both the elastic and plastic regions, and a high calcium content compared with the human adult. So, although the bone of the foetal axis deer is stiffer than that of children, its properties undergo substantial changes during ontogeny. The adult deer was younger than any of the children.

Summary

We measured the tensile strength, ultimate strain, work under the load-deformation curve, Young's modulus of elasticity, calcium content and porosity of specimens of bone from children, an adult man, a pregnant axis deer, *Axis axis* and her full-term foetus. The Young's modulus and strain to fracture of the foetus were intermediate between those of the children and the adult. The work that could be absorbed in the plastic region was less than in any of the human material. The calcium content of the foetal bone was considerably greater than that of the younger (three-year-old) child, which was itself most probably greater than that of a new-born baby. These differences are related to the habits of newly born deer and those of young children.

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