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OPTIMIZATION OF SKELETAL STRUCTURE IN VERTEBRATES (*)

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SUMMARY

Stresses due to bending moments generally predominate in long bones. They can be equalized along the length of the bone shaft if the bone tapers so as to make section modulus proportional to distance from the distal end. For marrow-filled bones, there is an optimum ratio of radius to wall thickness that minimizes mass for given strength, but different strength criteria give different optimum ratios. Increasing the strength of a bone reduces the probability of failure but increase the cost of growing the bone and the energy cost of moving it. A theory of optimum safety factors has been formulated but has not been used quantitatively because of the difficulty of expressing the cost of failure in the same currency as the other costs. A theory of optimum elastic stiffness successfully predicts the thicknesses of typical tendons. The possibility that the stiffness of bones is optimized, rather than their strength, is considered.

INTRODUCTION

Bones should be strong enough to withstand the forces that will act on them in life. They should not be unduly heavy, for a heavy bone (especially if it is a limb bone) is cumbersome : it may increase the energy cost of running or reduce the animal's maximum speed. How should bones be constructed, to be as light as possible for their strength ? What is the best compromise between strength and lightness ? We can expect evolution to optimize the proportions and thickness of bones whether it does so directly, by means of genes that specify bone dimensions, or indirectly, by genes that control the bone growth that occurs in response to the forces that the bone experiences (LANYON, 1981).

The forces on the distal end of a bone can be resolved into axial and transverse components. The axial component sets up compressive stresses that are uniform

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across any cross-section. The transverse component, however, tends to bend the bone and sets up stresses that range from a maximum compressive stress at one face to a maximum tensile stress at the other. Experiments in which bone stresses in running or jumping have been calculated from force plate records, or from the output of surgically implanted strain gauges, show for most of the long bones of limbs that transverse forces (that exert bending moments) are much more important generators of stress than are the axial forces (BIEWENER *et al.*, 1983, report an exception). Accordingly, in the following discussion, we will take account only of the bending moments that bones have to withstand.

BONE SHAPE

Long bones are generally tubular, with shafts that taper towards the distal end. How, precisely, should they be shaped?

The bending moment acting on a cross-section of a bone that is in equilibrium can be calculated by taking account only of forces on one side of the section : for example, distal to it. Muscle attachments are commonly restricted to the proximal ends of long bones, so for much of the length of the bone the bending moments can be calculated by taking account only of the transverse force on the distal end, and are proportional to the distance of the section from the distal end. The maximum stress due to a bending moment in a cross section can be calculatrd by dividing the bending moment by the section modulus, a geometric property of the cross section (see ALEXANDER, 1983b). A structure is only as strong as its weakest part so, to be as strong as possible for their weight, the shafts of bones should taper so

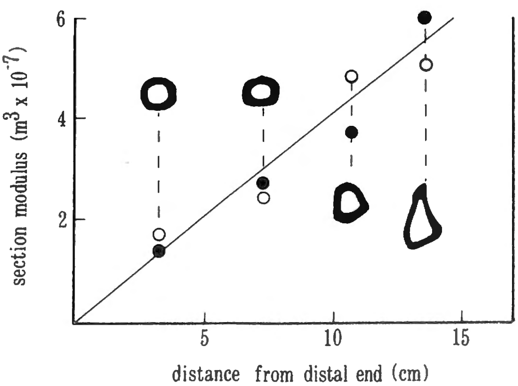

Fig. 1. — A graph of section modulus (both moduli are shown) against distance from the distal end of a dog tibia. The measured sections are illustrated with the anterior edge uppermost. From ALEXANDER (1975).

as to have section moduli proportional to distance from the distal end. Fig. 1 shows that this is approximately the case for the tibia of a dog, but ALEXANDER and VERNON (1975) found less good agreement in the case of a kangaroo tibia.

The strength of a bone in bending is proportional to the section modulus, and the weight per unit length to the cross-sectional area. The ratio of section modulus to cross-sectional area is greater for hollow tubes than for solid rods, so tubular structure gives strength with lightness. Accordingly, most long bones are tubular like the example of Fig. 1.

The ratio of the radius R of a tubular bone to the thickness t of its wall can have any value between one and infinity. What is the optimum? For a bone of given strength, as R/t increases (as the bone becomes a thinner-walled tube) the mass of the bone itself decreases but the mass of marrow within it increases. PAUWELS (1980) realized that this implied that there must be an optimum value of R/t, but CURREY and ALEXANDER (1985) pointed out a complication : the optimum value depends on how strength is defined. Fig. 2 shows that if bones of equal ultimate strength or impact strength are compared, the optimum value of R/t is 2.2. However, for bones of equal yield strength or fatigue strength the optimum is 3.0 and for bones of equal stiffness it is 4.0.

CURREY and ALEXANDER (1985) measured R/t for 228 long bones of 56 species. For terrestrial mammals they found values ranging from 1.0 to 3.7, with a marked mode at about 2. This is consistent with the hypotheses that bones are optimized for impact strength or for ultimate strength. As might be expected, much higher

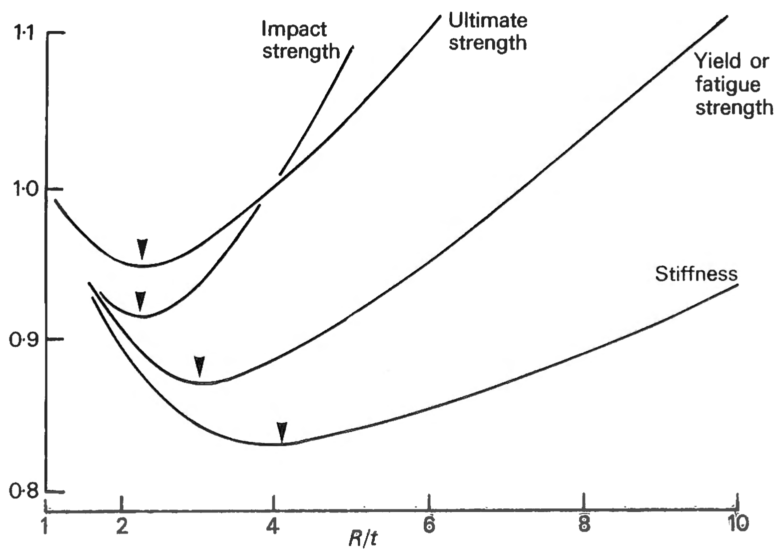

Fig. 2. — Masses of tubular marrow-filled bones (relative to the mass of a solid bone of equal length and strength) plotted against the ratio of radius to wall thickness. Curves are shown for several different strength criteria. From CURREY and ALEXANDER (1985).

values of R/T are common among such bird bones as are filled with gas instead of marrow.

FACTORS OF SAFETY

We have discussed how bones should taper, and what proportions their tubular cross sections should have. Next we ask, how strong should bones be ?

The factor of safety of an engineering structure is the ratio of the strength it is designed to have, to the maximum load it is expected to have to take. Engineers

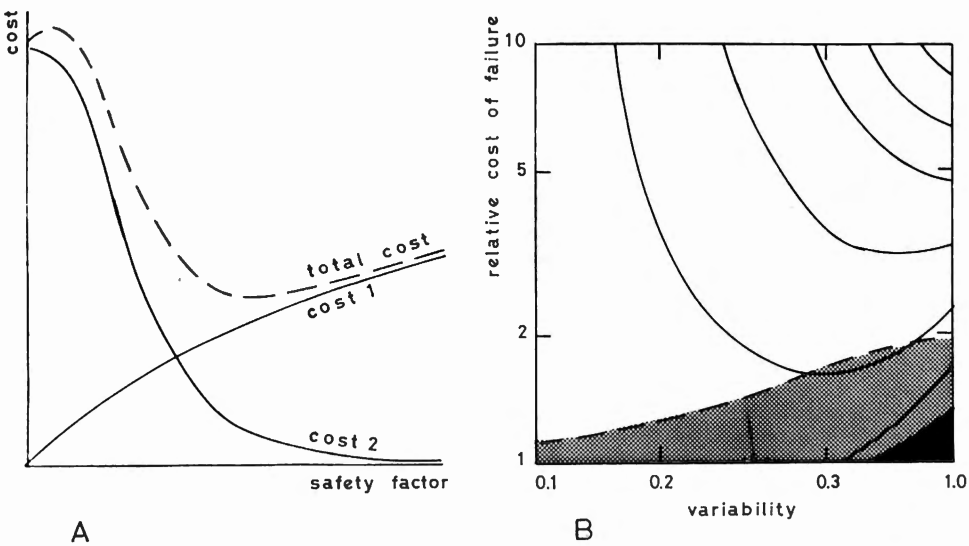

Fig. 3A. — Graphs of the costs associated with bones of different safety factors, according to the theory described in the text.

Fig. 3B. — A graph of the cost of failure against the variability of maximum loads, with contours showing the safety factor that minimizes total cost. Stippling indicates that the minimum is only a local one (the global minimum is at zero safety factor) and the black area indicates that the only minimum is at zero safety factor.

generally design structures with factors of safety much larger than one. This is necessary, to reduce the probability of failure to an acceptable level, because there is variation in actual strength, between structures built to the same design, and because maximum loads cannot be predicted precisely. Measurements of the stresses in bones in strenuous activities of various animals show that long bones commonly have factors of safety between 2 and 5 (Alexander, 1981 ; Biewener *et al.*, 1983). They nevertheless break : frequencies of healed fractures in long bones range from about 0.005 in birds to 0.03 in human (Amerindian) populations (BRANDWOOD *et al.,* 1986). Symmetry of strength between left and right bones of a pair in birds indicates that variability of strength is not a severe problem : bones need factors of safety principally on account of the unpredictability of the loads they have to bear (ALEXANDER *et al.,* 1984).

ALEXANDER (1981) presented a theory of optimum safety factors. I identified two costs that vary with safety factor (Fig. 3A). One, the cost of growth and use of the bone, increases with increasing safety factor : stronger bones require more energy and material for their growth and (because they are heavier) more energy for limb movements. The second cost, which decreases with inceasing safety factor, can be thought of as the notional cost of an insurance policy against failure : it is the probability P that failure will occur, multiplied by the cost of a failure. ALEXANDER (1981) gave reasons for modelling the cost of growth and use as proportional to (safety factor)$^{2/3}$ and the probability 1-P that the bone will *not* fail as a cumulative lognormal function of the safety factor.

This model has two parameters : the cost of failure (expressed as a multiple of the cost of growth and use for a safety factor of one) and the variability of maximum load (expressed as the standard deviation of the lognormal function). For many combinations of these parameters, the total cost has a minimum value for some non-zero safety factor (Fig. 3A). However, if the cost of failure is too low, the optimum safety factor is zero, and the bone can be expected to disappear in the course of evolution (Fig. 3B).

This model is regrettably difficult to apply quantitatively, because the costs of failure and of growth and use are generally most easily measured in different currencies (mortality and energy, respectively), and the exchange rate is unknown. However, some insight is given by the qualitative prediction that safety factors will be high when the cost of failure is high, especially if the variability of maximum load is also high (Fig. 3B). For example, the immensely thick leg bones of some moas (Dinornithes) may be due to the lack of any threat from predators, so that these herbivorous, flightless birds had little need to run. The cost of use for heavy leg bones was therefore low, making the relative cost of failure high (ALEXANDER, 1983a).

The theory of optimum safety factors was extended by ALEXANDER (1984) to take account of the danger of fatigue fracture.

OPTIMUM STIFFNES

To perform their functions, bones must be stiff as well as strong. A discussion of optimum stiffness for them is best introduced by an account of the theory of tendon stiffness which inspired it.

Some tendons serve as springs to save energy in running (ALEXANDER, 1988). Their elastic compliance is essential to this function, but the compliance of other tendons brings a disadvantage. Consider a muscle whose function is to develop a force and shorten, so as to move a joint through some required angle. If its tendon stretches, the muscle must shorten more to move the joint through the same angle. A muscle that has to shorten more needs longer muscle fibres (fibres with more sarcomeres in series) if it is to work only within the range of lengths at which it is capable of exerting large forces. If a tendon is made thinner (and so lighter), it will stretch more in use, and will require a muscle with longer fibres (which will therefore be heavier, for the same physiological cross-sectional area). Using this approach, KER *et al.* (1988) argued that the total mass of muscle plus tendon would be least if the cross-sectional area of the tendon was about 1/34 of the physiological cross-sectional area of the muscle. The stress in the tendon, when the muscle exerted its maximum isometric force, would then be about 10 MPa, only one tenth of the tensile strength of tendon. A survey of tendons in the legs and tails of various mammals showed that for the great majority of them, the ratio of tendon and muscle areas was close to this theoretical optimum. Tendons that serve as springs in running, however, are much more highly stressed. CUTTS *et al.* (1991) found that the thickness of tendons in a human forearm were close to the theoretical optimum.

ALEXANDER *et al.* (1990) applied the same reasoning to long bones. A slender bone is light but is also relatively flexible. Because it bends, muscles must shorten more to bring the distal end of the limb to a required position. To be capable of shortening more, the muscle requires longer fibres, so must be heavier. Reasonable assumptions about the properties of bone and muscle led to the conclusion that the total mass of bone plus muscle could be least, if the thickness of the bone were such that peak stresses of ± 70 MPa acted in each cross-section, when the muscles exerted their maximum isometric force.

Peak stresses of around ± 70 MPa are indeed commonly found in limb bones, in strenuous activities (ALEXANDER *et al.*, 1990). It would however be wrong to conclude at this stage that bone stiffness rather than bone strength is optimized. Such stresses may well result from selection for optimum safety factor : they correspond to a safety factor of about three.

CONCLUSION

The examples in this paper show how plausible models predict optimum proportions for bones. We should not ask simply whether a bone is strong enough for its function, or whether it is as light as possible. Rather, we should ask whether its dimensions are optimal.

Unfortunately, the predictions of the models are ambiguous. The optimization model for tubular proportions predicts different ratios of radius to wall thickness, depending on how strength is defined (Fig. 2). It has not yet been possible to apply the theory of optimum safety factors quantitatively, because exchange rates between currencies are unknown. The theory of optimum stiffness leads to a clear prediction, but the agreement between observed and predicted stresses may be coincidental.

The compositon of bones may vary, as well as their dimensions, leading to differences in mechanical properties (CURREY, 1984). A complete theory of bone design would seek to optimize composition as well as dimensions.

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