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J. R. Soc. Interface 2007 **4**, 127-135
doi: 10.1098/rsif.2006.0166

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Variability of the mechanical properties of bone, and its evolutionary consequences

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The relative variabilities (coefficient of variation (CV)) of 10 different mechanical properties of compact bone were determined from 2166 measurements. All measures of variability were made on a minimum of four specimens from any bone. Three pre-yield properties had a CV of about 12%. Six post-yield properties had CVs varying from 24 to 46%. Pre-yield properties increase as a function of mineral content, whereas post-yield properties decrease. These differences give insight into mechanical phenomena occurring at different stages during loading. Furthermore, the fact that some properties are more tightly determined than others has implications for the optimum values set by natural selection. This assertion is made more rigorous using a simple mathematical model for the evolutionarily optimal allocation in a trade-off where one property is imprecisely determined. It is argued that in general the optimum will be biased in favour of the more tightly determined properties than would be the case if all properties had the same CV.

Keywords: bone; variability; mechanical properties; evolutionary optima

1. INTRODUCTION

The objects of the work described in this paper are to measure the variabilities of various mechanical properties of compact bone, to determine to what extent they are different, and to suggest mechanical reasons for such differences as might appear. Furthermore, we consider the implications of such differences for the evolutionary optimization of these properties.

Most of the different mechanical properties of bone, such as Young's modulus, strain at failure, impact energy absorption and so on, cannot be compared directly but a few, such as strain at yield and ultimate strain, can be compared. This does not mean, of course, that variations in properties cannot be related, or one cannot be expressed as a *function* of another, and useful insights may often be gained by doing so. For instance, except for very highly mineralized bone, bending strength can be rather well expressed as a linear function Young's modulus (Currey 1999). However, the actual mechanical properties, say, bending strength and impact energy absorption, cannot be directly compared because they are measured in different units.

Nevertheless, the *variability* of different properties can be compared directly, and this, too, may give useful insight into the processes going on in the material during loading. For instance, structure-insensitive properties are those which are barely influenced by small inhomogeneities in microstructure or macrostructure (Ashby 2004). Young's modulus is structure

insensitive. On the other hand, many mechanical properties are very much influenced by small differences in the structure. A brittle material will be much weakened if it harbours small flaws. Materials affected by such things are said to be structure-sensitive for that property. As a result of this feature, structure-insensitive properties are likely to be less variable than structure-sensitive ones.

There are two main ways of expressing the variability of a mechanical property. One is the 'coefficient of variation', the other is the 'standard deviation of the logarithm of the values'. The coefficient of variation (standard deviation/mean) gets over the problem that the size of the standard deviations tends to be proportional to the mean size of the property itself, i.e. the data are heteroscedastic (Rice 1995). The coefficient of variation will be called 'CV' hereafter in this paper and will be reported either as an actual value or as a percentage. The standard deviation of the logarithms gets over the problem of heteroscedasticity directly. If properties with larger 'central tendencies' have larger variances for that reason alone, then the variance of the logarithms will be unaffected by this. The values 8, 9, 10, 11 and 12 have a mean of 10 and a standard deviation of 1.58, giving a CV of 15.8%. The values 800, 900, 1000, 1100 and 1200 have a mean of 1000 and a standard deviation of 158, again giving a CV of 15.8%. However, the logarithms (to the base 10) of these sets of numbers, although having quite different means of 1 and 3, both have a standard deviation of 0.070. Thus, the difference in the absolute values of the numbers has no effect on their standard deviations.

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Table 1. The sample sizes and origins of the specimens. The columns are in increasing order of mean CV as shown in table 2. The cells give the number of bones used to give a value for variability, and (in parentheses) the total number of specimens used. The same bones, and usually the same specimens, were often used to produce values for several different mechanical properties. E_B , Young's modulus in bending; BS, Bending strength; E_T , Young's modulus in tension; S_T , Tensile strength; Imp_{SLOT}, Impact energy of slotted specimens; W_B , Work in bending; ε_{ULT} , Ultimate strain; Wf, Work of fracture in bending; W_T , Work in tension; Imp, Impact energy absorption of unslotted specimens.

| origin | E_B | BS | E_T | S_T | Imp _{SLOT} | W_B | ε_{ULT} | Wf | Imp | W_T |
|---------------------|----------|----------|----------|----------|---------------------|---------|---------------------|----------|----------|----------|
| bovine | 12 (115) | 7 (71) | 3 (18) | 3 (18) | 2 (11) | 3 (21) | 3 (18) | 5 (44) | 2 (12) | 3 (18) |
| horse | 4 (67) | 1 (9) | 1 (7) | 1 (7) | 1 (11) | — | 1 (7) | 1 (7) | 1 (40) | 1 (7) |
| human | 3 (81) | 3 (81) | 3 (12) | 3 (12) | 1 (4) | 3 (81) | 3 (12) | — | 42 (247) | 3 (12) |
| various vertebrates | 38 (246) | 16 (118) | 25 (148) | 25 (148) | 4 (16) | — | 25 (148) | 22 (128) | 4 (16) | 25 (148) |
| total | 57 (509) | 27 (279) | 32 (185) | 32 (185) | 8 (42) | 6 (102) | 32 (185) | 28 (179) | 49 (315) | 32 (185) |

The standard deviation of the logged values of the mechanical properties will be called 'SDLOGS' hereafter in this paper. CV has an intuitive clarity, which the standard deviation of logarithms does not. By taking a first-order Taylor series expansion (Rice 1995), it may be shown that SDLOGS and CV times a scaling constant are approximately equal, provided the standard deviation is much smaller than the mean. For the data used in this paper, it will be shown that there is a proportional, linear and very tight relationship between the values of CV and SDLOGS.

The variability of estimated values of mechanical properties has two different sources: the variability associated with the specimens themselves and the experimental errors in determining the properties. These latter are not of primary concern in the present work but will, of course, tend to contribute to the apparent variability of the mechanical properties. Worse, the contribution of experimental error to the total variability may be different for different mechanical properties. This matter is dealt with in §4 and appendix B; suffice it to say here that experimental error almost certainly does not significantly affect the findings.

2. DATA AND METHODS

The mechanical properties whose variability is reported here are as follows. (The wording in square brackets refers to the notation in figure 2, if different, and in tables 1–4.)

Young's modulus of elasticity, determined in bending [E (bending), E_B]

Bending strength [BS]

Young's modulus of elasticity, determined in tension [E (tension), E_T]

Tensile strength [S_T]

Impact energy absorption of slotted specimens [Impact slot, Imp_{SLOT}]

Ultimate strain in tension [Ultimate strain, ε_{ULT}]

Work in bending [W_B]

Work of fracture in bending [Work of fracture, Wf]

Work in tension [Work in tension, W_T]

Impact energy absorption of unslotted specimens [Impact, Imp]

The material used for this work is from large datasets produced in JDC's laboratory. The species and bones

Table 2. Summary of results arranged in increasing order of mean percentage CV. The data points are the CVs for the individual bones. As an example, the value for the mean CV for bending strength is the mean CV for the 27 bones, using 279 specimens in all (sample sizes are given in table 1).

| property | mean CV |
|------------------|---------|
| E (bending) | 11.2 |
| bending strength | 11.2 |
| E (tension) | 12.8 |
| tensile strength | 16.7 |
| impact slot | 24.4 |
| work in bending | 28.6 |
| ultimate strain | 29.2 |
| work of fracture | 33.8 |
| impact | 37.5 |
| work in tension | 46.0 |

used are set out in appendix A. None of these datasets were originally collected in order to study variability. The methods used are not detailed here, but can be found in the original literature (Currey 1988 (Young's modulus in tension, Tensile strength, Ultimate strain, Work in tension, Work in bending, Young's modulus in bending, Bending strength, Work of fracture); Currey *et al.* 2004 (Impact energy)). All specimens were of roughly the same size.

It should be noted that work in bending and work in tension measure the amount of work done in bringing a specimen to the point where it fractures, usually catastrophically. The catastrophic fracture is caused by the large amount of strain energy which can be released to drive the crack forward. Work of fracture, on the other hand, using the method of Tattersall & Tappin (1966), measures the work needed to drive a crack through a specially shaped specimen, which is always essentially in equilibrium, i.e. there is never any excess strain energy to drive the crack forward uncontrollably. Work of fracture measures the work necessary to form two new broken surfaces.

Table 1 gives information on the sample sizes and provenance of the specimens. Three large mammalian species are given special attention. The unit of study was the individual bone. For instance, the values for tensile strength for various species include data from 32 different bones, using a total of 185 specimens.

Table 3. ANOVA table for the two-way model with the factors mechanical property and species, and the interaction between these factors. The *p*-values show that the two factors are highly significant. This implies that the mean (natural log) CV differs across mechanical properties and across species. However, the interaction term is not significant, implying that the size by which the mean (natural log) CV differs across mechanical properties does not vary with species. That is to say, we need to adjust the mean (natural log) CV for specimens of different species (e.g. horse and human), but the size of this adjustment is the same for properties of all types (e.g. those determined in bending strength and those determined in work in tension).

| source | degrees of freedom | sum of squares | mean square | F-ratio | p-value |
|---------------------|--------------------|----------------|-------------|---------|-------------|
| mechanical property | 9 | 91.5 | 10.2 | 54.5 | $<10^{-15}$ |
| species | 25 | 22.0 | 0.9 | 4.7 | $<10^{-9}$ |
| interaction | 103 | 23.6 | 0.2 | 1.2 | 0.118 |
| error | 165 | 30.8 | 0.2 | | |
| total | 302 | 167.9 | | | |

All values of variability of any individual bone were based on a sample size of four or more.

What one takes as a unit of study must be arbitrary. To take all values for a species would be too broad, because there might be differences in age and other variables. Even to take together values for different bones from the same animal would obscure possible different mechanical functions of different bones. The specimens used here were usually *not* taken along the lengths of the long bones, which might have different amounts of mineralization, but from the middle only. Even so, it is possible that, say, the anterior part of the bone might have a somewhat different function from the posterior part, with resulting differences in its mechanical properties which would add to the apparent variability. Thus, this cause of differences *within* bones should be borne in mind in reading what follows below.

3. RESULTS

(a) Relationship between CV and SDLOGS

Figure 1 shows the relationship, on logged axes. It is clearly extremely tight. The regression equation is

$$(\log CV) = 2.31 + 0.965(\log SDLOGS),$$

or, taking antilogs,

$$CV = 204 \times (SDLOGS^{0.965} \times R^2) = 98.1\%.$$

The value of the regression coefficient, 0.965, is very close to unity, and CV and SDLOGS are very nearly proportional to each other, in agreement with Rice (1995).

(b) Relationships between the mechanical properties and their variability

Table 2 shows a summary of the results arranged in increasing order of mean CV. The medians of the CVs (data not shown) are similar to the means, and were in a different order only once (work in bending and

Table 4. Table of predicted mean CVs from the ANOVA model and *p*-values for the various mechanical properties shown in table 2. The predicted values are different from the 'raw' values shown in table 2 because in this table the effect of species is removed. The *p*-values test a null hypothesis that the mean CV of the mechanical property is not different from the mean CV of *E* (bending). Thus, for instance, the CV for ultimate strain has a *p*-value less than 10^{-15} , and we reject the null hypothesis and conclude that the CV of ultimate strain is significantly different from the CV of *E* (bending).

| mechanical property | predicted CV | p-value |
|---------------------|--------------|-------------|
| <i>E</i> (bending) | 9.4 | — |
| bending strength | 9.4 | 0.989 |
| <i>E</i> (tension) | 10.5 | 0.298 |
| tensile strength | 13.8 | 0.0003 |
| impact slot | 22.8 | $<10^{-5}$ |
| work in bending | 27.3 | $<10^{-6}$ |
| ultimate strain | 24.9 | $<10^{-15}$ |
| work of fracture | 27.0 | $<10^{-15}$ |
| impact | 38.1 | $<10^{-15}$ |
| work in tension | 38.9 | $<10^{-15}$ |

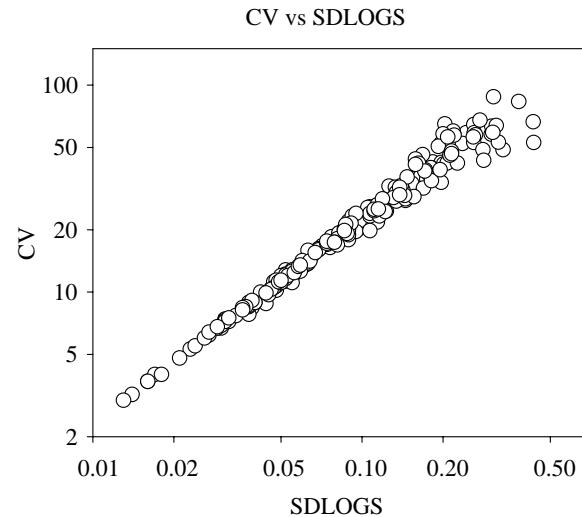


Figure 1. Relationship between values of the CV and the SDLOGS of all the properties estimated in all the bones. Note the logged axes.

ultimate strain). Means and medians of SDLOGS are not reported here, but were both in the same order as the CV medians. Figure 2 shows a box-and-whisker plot for mean CV. Both CV (figure 2) and SDLOGS (data not shown) illustrate very similar patterns of variability with mechanical property, and only CVs are considered in the subsequent statistical analysis.

To quantify how variability was influenced by mechanical property, the technique of ANOVA was used. In order for the standard assumptions of ANOVA to be met (see Rice 1995), CVs were transformed using natural logarithms before analysis. Investigation showed that the standard assumptions were met after this transformation. A two-way ANOVA was used with mechanical property and the origin of the specimen (i.e. the species from which it was taken) as factors. Table 3 shows that both factors were highly significant, but the interaction between them was not significant.

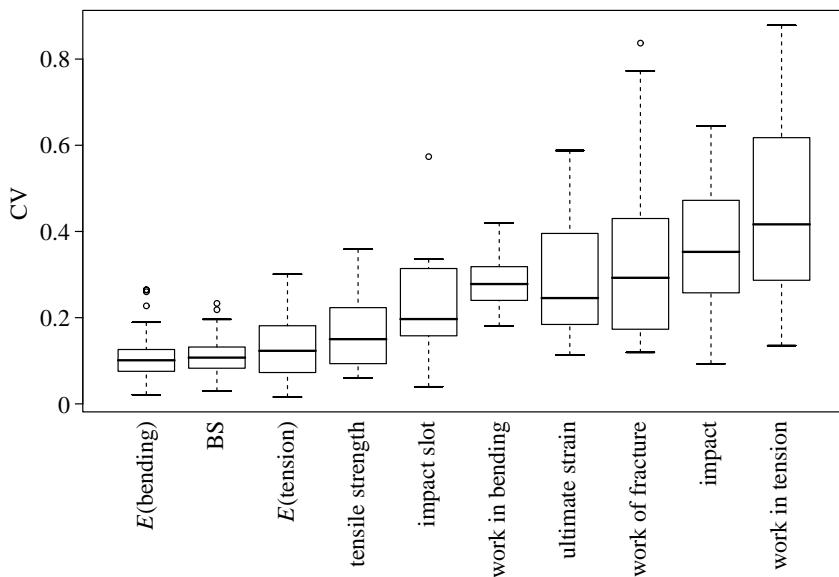


Figure 2. Box-and-whisker plots of CV for the various mechanical properties.

There were insufficient data to include factors relating to the type of bone within a species, the age of the animals, etc. However, it is worth commenting that the bones of the 103-year-old Galapagos tortoise had variabilities that were broadly the same as those of much younger animals (data not shown).

Energy absorption in impact of unslotted specimens, work of fracture in quasi-static loading and work under tensile stress-strain curve had mean CVs at least twice that of estimates of elastic modulus and bending strength (see table 2). However, the species has a significant effect on CV (table 3). In the analysis of table 2, the effect of species is confounded with the effect of mechanical property. Table 4 reports the predicted CVs for mechanical property and their associated *p*-values from the two-way ANOVA involving mechanical property and species (without interaction). Young's modulus of elasticity in bending was taken as the (arbitrary) reference property. Hence, the *p*-values provide an assessment of which mechanical properties have CVs significantly different from *E*(bending), while controlling for species. Generally, the probability values decrease going down the rows in table 4; this is because the rows were ordered in increasing mean values of CV, making such a decrease likely, but by no means certain.

4. DISCUSSION

(a) Measurement error

Before dealing with the question of the variability of the mechanical properties, we must deal with the question of measurement error. Measurement (observer) error will inevitably inflate the values of CV and SDLOGS above the 'true' values. Therefore, the question arises: is the measurement error likely to be a significant portion of the total variation and, perhaps more importantly, is it likely that it will inflate the CVs of some properties more than those of others? The two main sources of experimental error are the error produced in determining the size and shape of the specimen, and the error

produced in determining the value of the variable being measured (load, work, strain, etc.). This matter is dealt with in appendix B, and the results are summarised in table 5. The implication of this necessarily rather simple analysis is that measurement error is a negligible contributor to overall variation and, furthermore, the larger values of variability are *not* associated with larger measurement errors.

(b) The variation in variability between different mechanical properties

In this part of the discussion we shall refer to 'variability'. The properties with the lowest variability are bending strength, Young's modulus determined in both bending and tension, and tensile strength. Table 4 shows that bending strength and Young's modulus (determined in tension) do not have a significantly different CV from Young's modulus determined in bending. Tensile strength is significantly different from Young's modulus in bending at the 0.1% level ($p=0.0003$); however, the *p*-values for the remaining mechanical properties are all orders of magnitude smaller ($p \ll 10^{-5}$). Thus, the mechanical properties appear to divide into two groups; bending strength and Young's modulus (and possibly tensile strength) forming one group of properties with lower variability, and impact with slot, ultimate strain, work in bending, work of fracture, impact no slot and work in tension forming a second group with higher variability.

These differences in variability are what would be predicted from the processes that produce the mechanical properties. Young's modulus is a classic structure-insensitive property, being barely affected by small variations in the presence of flaws and inhomogeneities in the material (Ashby 2004). It might seem strange that bending and tensile strengths should have a low variability, but it has been shown that the bending strength of bone is very tightly correlated with Young's modulus. This is probably because bending strength is closely correlated with yield stress, and yield stress is

Table 5. Estimates of the partitioning of variability between the intrinsic variability of the specimens and the experimental error. ‘Refined estimate’ is described in appendix B.

| property | CV of property estimate (%) (means) | estimated CV of measurement error (%) | refined estimate of CV of property (%) |
|---------------------|-------------------------------------|---------------------------------------|--|
| BS | 11.2 | 0.9 | 11.1 |
| E_B | 11.2 | 1.6 | 11.1 |
| E_T | 12.8 | 0.6 | 12.8 |
| S_T | 16.7 | 0.6 | 16.7 |
| ImpSLOT | 24.4 | 1.2 | 24.4 |
| W_B | 28.6 | 0.6 | 28.6 |
| ε_{ULT} | 29.2 | 0.8 | 29.2 |
| Wf | 33.8 | 0.6 | 33.8 |
| Imp | 37.5 | 1.0 | 37.5 |
| W_T | 46.0 | 0.8 | 46.0 |

proportional to the product of yield strain and Young’s modulus. Yield strain is nearly invariant in compact bone, and therefore bending strength will be closely related to Young’s modulus (Currey 1999). The three least variable properties (including bending strength) can be considered to be properties that are determined by the behaviour of bone up to yield. Furthermore, tensile strength is probably somewhat like bending strength in that it is highly correlated with yield stress (though not as tightly as is bending strength) which in turn is closely determined by Young’s modulus.

After yield, damage is occurring in the bone, and hence the precise positioning of flaws and inhomogeneities in relation to any potentially dangerous crack becomes important. The post-yield properties do indeed have higher values of CV than the pre-yield properties (table 2) and the difference is even more marked with ‘predicted’ values (table 4).

Ultimate strain is a component of the work in tension, and so it is also likely to be very variable. It should not, of course, be as variable as total work (area) under the load-deformation curve, (nor is it) because it is only one component, the ‘X-axis’ component as it were, of an area.

(c) Uncertainty, trade-offs and evolution

The data presented here show that variability in pre-yield properties of bone is less than that of post-yield properties. The major determinant of the mechanical properties of bone stressed principally in the longitudinal direction, as here, is the mineral content, though other variables such as porosity, histology and anisotropy also have an effect (Reilly & Burstein 1975; Liu *et al.* 2000; Currey 2006, table 4.3). The pre- and post-yield properties are strongly influenced by bone mineral content, and in general in opposite directions, i.e. bone cannot be both very stiff and very tough.

Here, we take ‘mineral’ (m) to be the generic term for factors affecting mechanical properties, since it is by far the most important. Since an animal requires its bones to be both ‘stiff’ and ‘tough’, it is natural then to ask if the observed variability might influence the optimal mineral content. It seems plausible that evolution

might encourage the animal to use an amount of mineral appropriate for more predictable (pre-yield) properties, rather than for less predictable properties.

In what follows, little attempt has been made to assign realistic values for fitness, variability and so on. Instead, we develop the *principle* of how different amounts of uncertainty in mechanical properties will affect the evolutionarily optimal mineral content. The argument is illustrated, and broadly quantified, by considering a simple mathematical model. This is first presented as a purely deterministic system, before being contrasted with a stochastic model which accounts for uncertainty.

Suppose an individual organism’s genotype causes it to use a certain amount of mineral m , where m is between 0 and 1. (The values of mineral content found in bone are by no means as low as 0, so that ‘0’ represents some arbitrary minimum value of mineralization. The argument is unaffected.) This mineral governs the individual’s fitness in respect to two properties, S and T : S is proportional to m , and T to $(1-m)$. Choosing the ‘best’ m is therefore a trade-off between properties S and T . In the context of this paper, with m referring to bone mineral content, S can be thought of as pre-yield stiffness and T as post-yield toughness. Assume that an individual’s total fitness F_d (subscript d refers to the deterministic model) is the product of S and T ,

$$F_d = m(1-m). \quad (4.1)$$

Here, ‘fitness’ is necessarily defined without the precision required by a full genetic description; it simply quantifies the likelihood that an individual will reproduce successfully to generate viable offspring in the subsequent generation. The optimal choice of m , m_d say, is that which maximizes F_d . One can therefore use equation (4.1) to assert that $m_d=0.5$, with equal allocation to S and T . Indeed, $m_d=0.5$ can be shown to be the evolutionarily stable strategy (ESS; Maynard-Smith 1982) for this simple deterministic model.

Now modify the model to take into account the fact that property T is not precisely determined by $(1-m)$, but is instead subject to uncertainty; a particular individual’s T value is a random variable with mean proportional to $(1-m)$ and some finite variance, while S is perfectly determined by m . One can readily show that, in order to maximize the *average* fitness of an offspring, a parent should again adopt the deterministic ESS, i.e. $m=0.5$. However, this conclusion is misleading.

Darwinian ‘survival of the fittest’ cares little for average individuals. In reality, the fitter the offspring, the more likely it is to survive to become a parent in the next generation. Suppose, therefore, that in any generation only a proportion p of individuals, assumed for the sake of simplicity to be those individuals with the largest fitness, become parents in the next generation.

In this stochastic context, an individual’s fitness can be described by

$$F = m(1-m + \xi), \quad (4.2)$$

where the random variable ξ , with zero mean and probability density function $f(\xi)$, represents the uncertainty in T . Each individual’s fitness is therefore an independent random variable with the same expected

value as in the deterministic model. The ESS is then the choice of m which maximizes the fitness of the fittest proportion p of the offspring. Mathematically, the best choice, m^* , is that which maximizes

$$\int_x^\infty m(1-m+\xi)f(\xi)d\xi, \quad (4.3)$$

where x is chosen so that the integral in equation (4.3) only considers the fittest proportion p of the individuals. From equation (4.2), the fittest individuals are those with the largest ξ values, so that the value of x is calculated by

$$\int_x^\infty f(\xi)d\xi = p. \quad (4.4)$$

It can then be shown that

$$m^* = m_d + \frac{1}{2p} \int_x^\infty \xi f(\xi)d\xi. \quad (4.5)$$

Since the integral in equation (4.5) is always positive (ξ has zero mean overall, and this integral can be regarded as the mean of the largest proportion p of realizations of ξ), this implies that m^* exceeds m_d by an amount which increases with the intraspecific competition for survival in the next generation ($1/p$).

Figure 3 illustrates a concrete example. For a given value of m , an individual's T is given by $(1-m+Y)$ where Y is a uniform random variable distributed uniformly in $[-\varepsilon, \varepsilon]$, with $S=m$ as previously. It is assumed, arbitrarily, that each individual has 10 independent offspring, and that only the fittest 10% of the offspring population survive to parent the next generation (i.e. $p=0.1$). Figure 3a shows the basic trade-off, showing S (deterministic) and T (variable, with notional 95% confidence intervals) as functions of m , together with m_d and m^* . In the mathematical framework outlined above, $f(\xi)=1/(2\varepsilon)$ on the interval $[-\varepsilon, \varepsilon]$ and is zero elsewhere. Equation (4.4) can then be solved to give $x=4\varepsilon/5$. Substituting this into equation (4.5) then reveals

$$m^* = \frac{1}{2} + 5 \int_{4\varepsilon/5}^\varepsilon \left(\frac{\xi}{2\varepsilon} \right) d\xi = \frac{1}{2} \left(1 + \frac{9\varepsilon}{10} \right). \quad (4.6)$$

Figure 3b shows the value of m^* as predicted by equation (4.6), for various values of uncertainty ε : the accompanying box-and-whisker plots show the outcome of stochastic individual-based simulations of the same process. (We used a classic genetic algorithm: 100 individuals each have 10 offspring inheriting its parent's $m \pm$ some noise (up to 0.1% of m); individual fitnesses are allocated with deterministic S and variable T as above; the fittest 100 offspring survive to become parents in the next generation; simulation initialized with random m values in $[0, 1]$ and iterated over 10 000 generations.)

The above argument shows that, in the real stochastic world, organisms need not evolve to be the fittest *on average*; the best strategy maximizes the fitness of those individuals fortunate enough to survive. The simple example of figure 3 shows that this effect can in principle be large, especially when both variability and selection pressure are large. The idea is not new; Hamilton & May (1977) arrive at similar conclusions regarding apparent sub-optimality when considering

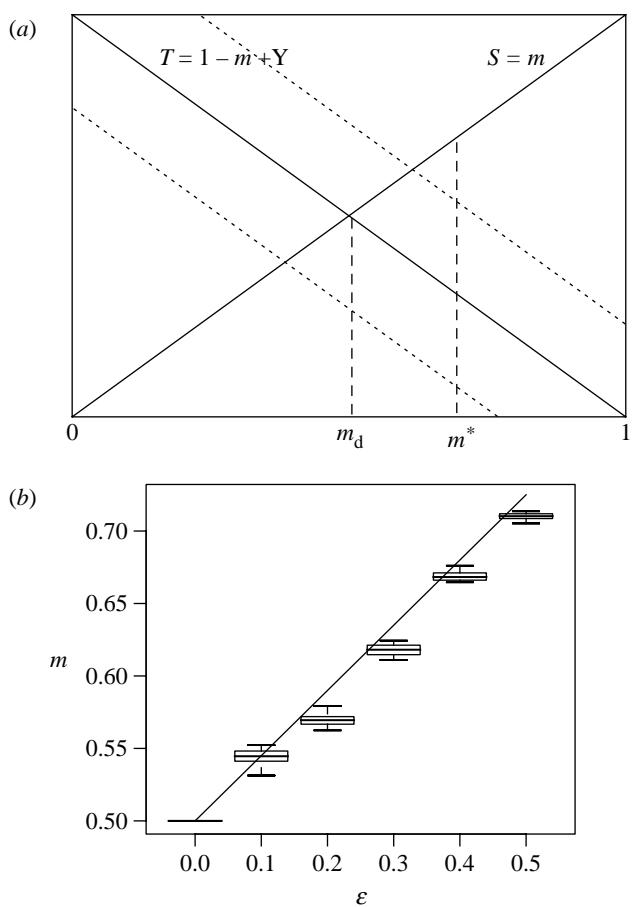


Figure 3. (a) Schematic diagram of the trade-off between properties S (deterministic) and T (stochastic; 95% confidence intervals shown by sloping dotted lines), showing the deterministic ESS m_d , and the ESS for the stochastic system m^* . (b) Theoretical predictions (straight line, from equation (4.6)) and stochastic individual-based model outputs (box-and-whisker plots) for m^* ($p=0.1$, ε between 0 and 0.5, see text for details).

dispersal models; Yoshimura & Shields (1987, 1992) also identify 'false optima' in explicitly stochastic models of dispersal and clutch size; similar theories may be applied in stochastic environments (Yoshimura & Clark 1991). Since the search for optimality lies at the heart of most evolutionary modelling (Alexander 1996), this simple message may be more widely applicable, for example to ESS theories, adaptive dynamics (Dieckmann & Law 1996) and foraging (Pitchford *et al.* 2003). In the case of bone, a simulation approach combining deterministic bone growth with a genetic algorithm to describe evolution (Nowlan & Prendergast 2005) suggests that bones may not evolve to precisely optimal values, although they do come close. Our results suggest that if stochastic elements of growth and stress were incorporated into such a model, then the results would appear more strongly non-optimal in comparison with deterministic predictions.

The simple model may be readily generalized, or modified to incorporate more realistic trade-offs, uncertainties or survival probabilities, but its basic conclusions are unlikely to change: when faced with a trade-off between two properties, which are susceptible to different degrees of uncertainty, the optimum is to

over-invest in the more certain property than would be predicted by a deterministic model. The magnitude of this movement of the optimum increases with both uncertainty and selection pressure. In the case of bone's mechanical properties, these considerations need to be borne in mind, along with the variability data above, when one attempts to reverse engineer bone's mechanical properties and determine what natural selection has designed bone *for*!

Thanks to Jin Yoshimura, Calvin Dytham, Richard Law and Peter Mayhew for their discussions regarding evolutionary models, and to the late Kevin Brear for making the majority of the more than 2000 mechanical measurements. We also acknowledge the valuable comments of four anonymous referees.

APPENDIX A.

List of species and bones used.

| | |
|---|-------------------------------------|
| alligator <i>Alligator mississippiensis</i> | femur |
| atlantic white-sided whale | rib |
| <i>Lagenorhynchus acutus</i> | |
| axis deer <i>Axis axis</i> | tibia |
| bovine <i>Bos taurus</i> | femur; metatarsus, tibia |
| crane <i>Grus antigone</i> | metatarsus, ossified tendon, radius |
| donkey <i>Equus caballus</i> | radius |
| dugong <i>Dugong dugon</i> | scapula |
| african elephant <i>Loxodonta africana</i> | tusk dentine |
| fallow deer <i>Dama dama</i> | tibia |
| flamingo <i>Phoenicopterus ruber</i> | tarsometatarsus, tibiotarsus |
| galapagos tortoise <i>Geochelone midas</i> | femur; fibula, humerus, tibia |
| hippopotamus <i>Hippopotamus amphibius</i> | femur |
| human <i>Homo sapiens</i> | femur |
| horse <i>Equus caballus</i> | femur, radius |
| king penguin <i>Aptenodytes patagonica</i> | humerus |
| leopard <i>Panthera pardus</i> | femur |
| polar bear <i>Thalarctos maritimus</i> | femur |
| rhinoceros <i>Rhinoceros unicornis</i> | humerus |
| roe deer <i>Capreolus capreolus</i> | femur |
| seal <i>Halichoerus grypus</i> | tibia |
| tiger <i>Panthera tigris</i> | femur |
| wallaby <i>Protemnodon rufogrisea</i> | tibia, tarsus |
| walrus <i>Odobenus rosmarus</i> | humerus |

APPENDIX B.

B.1. Error propagation

The methods by which errors are summed or multiplied as one proceeds through calculations are called ‘error propagation’ (Taylor 1982). The rules for combination are:

(i) If CVs are added or subtracted, the total CV is given by

$$CV_A + CV_B = CV_A - CV_B = (CV_{A^2} + CV_{B^2})^{1/2}.$$

(ii) If CVs are multiplied or divided together

$$CV_A \times CV_B = CV_A / CV_B = (CV_{A^2} + CV_{B^2})^{1/2},$$

as before.

(iii) If a CV is raised to a power n , the CV is $n(\text{CV})$.

It can be seen that in cases (i) and (ii), if there is much difference between the CVs, then the total CV will be dominated by the larger CV.

We can use these relationships to estimate the effects of the errors of measurements on the estimates of the CVs of the various mechanical properties. We shall discuss these in the order of increasing variability of the final value, Young's modulus measured in bending being least with a mean CV of about 11%, and work under tensile stress strain curve being greatest with a mean CV of about 45%, with corresponding differences in the standard deviations of logged values.

B.2. Estimates of measurement error

Repeated (40) measurements were made of the depth and breadth of several specimens. In each specimen, the measurements were made on the same place, so these were repeated measurements, and indicated the size of the error made in actually performing the measurement. The mean CV (which varied very little from specimen to specimen) was $0.00359 = 0.36\%$, say 0.4%. This can be taken as the error introduced by the measurement of the cross-sectional dimensions of the specimens. Ten measurements of depth and breadth were also made *along* several specimens, to see how far they differed from being prismatic. Remarkably, the CV of these measurements was not greater than that of repeated measurements at the same place, showing that the specimens were, indeed, very nearly prismatic, and that no account need to be made of departures from being prismatic in calculating overall estimates of measurement CVs. Measurements of the length between the knife-edges of the extensometer used to determine deformation had a somewhat higher CV, say 0.6%, and repeated measurements of the apparent deformation gave a CV of 0.4%.

B.3. Young's modulus in bending

The formula for Young's modulus measured in three-point bending is $E = \text{load} \times L^3 / 48 \times \text{deflection} \times I$. It is clear that results using this formula may be severely affected by measurement errors. *Load/deflection* can be measured reasonably consistently, because in bending, after the toe region, the trace is very gently curved. It is traditional to measure the tangent to the curve at the steepest point. This can be determined reasonably precisely, and we shall assume CVs of 0.1% for both load and deflection. L , although appearing as a cubed term, would be precisely the same for all specimens in a bone; however, we assume a CV of a single measure of length of 0.1%. I having a depth³ term is a potent source of error.

Using similar procedures as for bending strength, one arrives at a value of CV for load/ L^3 (deflection) $\times I$, $(0.001^2 + (3 \times 0.001)^2 + 0.001^2 + (3 \times 0.004)^2 + (0.004)^2)^{1/2} = 0.016 = 1.6\%$.

B.4. Bending strength

The formula for bending strength is: bending strength $= Mc/I$, where M is the bending moment at failure; c is half the depth of the section and I is the second moment of area. The load at failure is easily measured precisely, and the gauge length also. Anyhow, the gauge length was identically the same for all the specimens measured on a particular bone, and so would have no effect on the variability. Giving these 'precisely' measured values, a CV of 0.1% would seem reasonable. Therefore, the value of M can be considered (from §B.2, above) to have a value CV of: $(0.001^2 + 0.001^2)^{1/2} = 0.0014 = 0.14\%$. As long as the specimen was reasonably prismatic (i.e. having the same cross-sectional shape along its entire length), which was true of all specimens discussed here, the remaining source of experimental error is the measurement of c/I . I has a depth³ term and a breadth term in it, so c/I has a depth squared term and a breadth term in it. Assuming a CV of 0.4% for these measurements (see above), the CV of c/I is $((2 \times 0.004)^2 + (0.004^2))^{1/2} = 0.0089 = 0.89\%$. The CVs 0.14 and 0.89% must be multiplied giving an overall value for the CV of $0.0090 = 0.9\%$ (note the relative unimportance of the length and load measurements in arriving at the final estimate).

B.5. Young's modulus in tension

Length, needed for determining the strain, was precisely determined (say CV = 0.1%), and the increase in length was determined by a contact extensometer (say CV = 0.1%). The specimens were as prismatic as could be made by grinding and polishing, and estimates of cross-sectional area varied little along the gauge length.

Value of CV for load/(length \times deflection \times breadth \times depth) gives

$$(0.001^2 + 0.001^2 + 0.001^2 + 0.004^2 + 0.004^2)^{1/2} = 0.0059 \approx 0.6\%.$$

B.6. Tensile strength

This is given by the load at failure, which could be precisely determined, divided by cross-sectional area. As long as the specimen is reasonably prismatic, it is only the cross-sectional area at the fracture point that is of concern. Calculation gives an estimate of CV of $(0.001^2 + 0.004^2 + 0.004^2)^{1/2} = 0.0057 \approx 0.6\%$

B.6.1. Impact strength with slot. The impact energy absorbed was calculated from the energy loss of a falling pendulum. The scale on the impact machine was somewhat coarser than on the other measuring devices, and tests using naive observers estimating the position of the pointer suggested that the CV for impact energy absorbed was about $0.008 = 0.8\%$. The cross-sectional

area at break would have the same size of errors as for specimens used for calculating tensile strength. The cutting of a slot resulted in the ligament area being slightly more difficult to measure than the cross-sectional area of an unslotted specimen. Again, the CVs would be of the order of $(0.008^2 + 0.004^2 + 0.008^2)^{1/2} = 0.012 = 1.2\%$.

B.7. Ultimate strain

This does not depend on specimen dimensions at all. The errors lie in the determination of the distance between the knife-edges of the extensometer, and the deformation from the hard copy output of the oscilloscope. Two CVs of errors, estimated to be 0.006 and 0.004, combine to give an error of $0.0072 \approx 0.8\%$.

B.8. Work in bending

The work was calculated from the area under the curve on the testing machine paper output. This could be measured with high precision. The cross-sectional area, which was the other measurement needed, was measured with the same precision as for the tensile strength. Assuming a CV for work of 0.001, this gives a value for overall CV similar to that of tensile strength: $0.0057 \approx 0.6\%$.

B.8.1. Work of fracture. The work was calculated from the area under the curve on the testing machine paper output. This could be measured with high precision. The cross-sectional area of the triangular ligament could not be measured with the same accuracy as the dimensions of the sides of unmodified specimen. We assume a CV of twice that of the measurements of breadth and depth (0.008). Therefore, the overall CV is $(0.001^2 + 0.008^2 + 0.008^2)^{1/2}$. These combine to give an error of $0.0114 \approx 1.1\%$.

B.8.2. Impact energy in unslotted specimens. This would be the same as for slotted specimens except that the depth, being of the whole specimen, could be measured more accurately. Thus, the error CV can be estimated as $(0.008^2 + 0.004^2 + 0.004^2)^{1/2} = 0.0098 \approx 1\%$.

B.9. Work in tension

Although these estimates are somewhat rough and ready, they do show that the CVs of the measurement errors are small compared with the overall CVs of the mechanical properties. Indeed, they are sufficiently small that, if §B.1. is used to produce a 'refined estimate CV' of the property:

$(\text{refined CV})^2 = (\text{property estimate CV})^2 - (\text{measurement error CV})^2$, they are shown to have virtually no effect on the refined estimate of the mechanical properties. (It is a rule of thumb in error propagation analysis that if one error term is an order of magnitude greater than another, the latter can be ignored.) Finally, table 5 also shows that the larger CVs are not associated with particularly large measurement errors.

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