ONTOGENETIC SCALING AND MECHANICAL BEHAVIOUR OF THE TIBIAE OF THE AFRICAN DESERT LOCUST (SCHISTOCERCA GREGARIA)

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Summary

Current models for scaling of skeletal morphology were examined to test their applicability to the ontogenetic growth of an exoskeletal animal, the African desert locust (Schistocerca gregaria). It was found that the tibial leg segments of both the mesothoracic (i.e. non-jumping) and the metathoracic (jumping) legs scaled in a manner that produced relatively longer, more slender skeletal elements as the animal grew. Metathoracic tibial length scaled to tibial diameter raised to the power 1.21. This result deviates both from isometric (i.e. geometric similarity) and distortive (constant stress, elastic similarity) allometric models.

The mechanical properties of the metathoracic tibiae were measured using a dynamic, three-point bending technique. The flexural stiffness of metathoracic tibiae scaled to body mass raised to the power 1.53. This was intermediate to the predictions made by constant stress and elastic similarity models. Thus, the mechanical properties scaled as predicted by mechanical scaling expectations in spite of the morphological developmental programme.

It may be that the thin-walled skeleton developed in the exoskeletal body plan has allowed a finer control over the distribution of load-bearing material in the leg. Such a distribution may be responsible for the observed increase in mechanical stiffness of legs that exhibit an unexpectedly spindly morphology. The rationale for the observed morphological programme may be a design that takes advantage of the inherent deformability of long, slender beams. Thus, it may be that the tibiae, which have been treated as rigid levers, are in fact flexible springs. Calculations indicate that the energy stored in the substantial deflection of the adult, metathoracic tibiae during a jump may be as high as 10% of the total kinetic energy of the jump.

Introduction

The study of the relationship between body size and skeletal morphology attempts to explain how morphological design accommodates the mechanical demands of support and movement (see, for example, Schmidt-Nielsen, 1984). Up
until now the general scaling models, or allometries, have been developed to
describe skeletal design in functionally equivalent, adult, endoskeletal animals
that differ only in size. These relationships have been tested with a variety of
interspecific comparisons between adults of closely related taxa (i.e. phylogenetic
scaling). One could also analyze the effect of scale in the development of an
individual and apply similar relationships (i.e. ontogenetic scaling). It is not clear,
however, whether the developmental programme in a single species produces a
series of *functionally equivalent* skeletal designs constructed from mechanically
equivalent materials (Carrier, 1983; Currey and Pond, 1989). For example,
Carrier’s (1983) observations of jack rabbits suggest that in vertebrate ontogeny
bone may vary in its material stiffness (i.e. modulus) by as much as an order of
magnitude. The same data also indicate that neonates, juveniles and adults may
not be functionally equivalent in their ability to locomote. However, if functional
equivalence is maintained across ontogeny, then it should be fair to ask whether
the existing models of scaling apply to that ontogenetic sequence.

In this study we have examined the ontogenetic scaling of the African desert
locust (*Schistocerca gregaria*), an animal with six discrete life history stages, or
instars, during which it increases in body mass by two and a half orders of
magnitude. This analysis is legitimately made in *Schistocerca gregaria* because this
ontogenetic sequence represents functionally equivalent individuals. That is, their
peak performance, manifest in jump distance, is maintained across the five
juvenile instars (Gabriel, 1985a).

The scaling analysis that we have performed on the skeleton of the locust
provides some interesting contrasts to the scaling relationships observed in
vertebrate designs in several respects: the locust is exoskeletal rather than
endoskeletal, changes of external dimensions occur in discrete steps rather than
continuously, and comparisons are made across the ontogeny of hoppers rather
than between closely related, adult walkers and runners. With these contrasts in
mind, we have examined the scaling in *Schistocerca gregaria* to see if there are
distinctive design principles employed in the jumping legs of the locust.

The structural consequences of isometry are well known (Galileo, 1638;
McMahon, 1984). The design scheme that results in isometry, the geometric
similarity model (GSM), correlates changes in mass with a single characteristic,
linear dimension. The general formulation scales the linear dimensions of length
diameter to mass raised to the one-third power. Allometries that predict
distortions in morphology with changes in size, such as the elastic similarity model
(ESM) or the constant stress similarity model (CSSM), rely on two characteristic
linear dimensions, length and diameter, which scale differently to body mass. In
the ESM, length scales to mass to the one-quarter power and diameter scales to
mass to the three-eighths power (McMahon, 1973). While in CSSM, length scales
to mass to the one-fifth power and diameter scales to mass to the two-fifths power
(McMahon, 1984). In either case, there is a trend towards relatively thicker,
stouter skeletal segments with increasing body size.

Bertram and Biewener (1990) have suggested that GSM may be an appropriate
scaling scheme for small animals, where breakage of the skeleton due to loading is unlikely. For small animals, having a skeleton sufficiently stiff to function in support and locomotion is probably the primary function of the skeleton. They also argue that in large animals, where loads are likely to exceed the breaking strength of geometrically similar skeletons, the morphology must change, or distort, to accommodate those loads. These loads are in general thought to be related in some direct fashion to body mass. ESM scaling seems to be observed in the skeletal design of ungulate limb bones (McMahon, 1975), although Bertram and Biewener (1990) suggest that CSSM may more adequately describe the scaling in the larger members of that data set. In any case, these observations have been made largely on endoskeletal animals, while very little has been said on the scaling of exoskeletal animals. Prange (1977) has shown that leg segments of the cockroach, Periplaneta americana, and the wolf spider, Lycosa lenta, scale very closely to GSM over an ontogenetic sequence.

Regardless of which morphological model is considered, it is assumed that the mechanical behaviour of a skeletal member can be inferred from morphological measurements. This seems to be a reasonable condition in the interspecific comparisons made among adult ungulates, for example (McMahon, 1975), where the material properties of calcified bone and the general method of employing that material are fairly uniform across the group. Ontogenetic changes in material properties of bone do occur (Currey and Butler, 1975; Carrier, 1983), uncoupling to some extent our ability to infer mechanical behaviour of the skeleton from its morphology. In insects, where the skeleton is also the integument and is not mineralized to nearly the same extent as bone, it is possible that the material properties of the skeleton can be modulated to meet the mechanical demands of increasing body size in ways that are fundamentally different from vertebrates. The cuticle in various parts of the locust exoskeleton shows a wide repertoire of mechanical properties (Jensen and Weis-Fogh, 1962; Vincent, 1975), which might suggest such a possibility. Hepburn and Joffe's (1974b) observation that normalized cuticular stiffness is maintained across instars would argue against the suggestion that the material properties of the cuticle are changing. However, insects are a diverse group, and it may be that some of them have developed different strategies for solving skeletal scaling problems.

While Bertram and Biewener (1990) have made a case for body size determining the appropriate scaling programme to follow, Bou et al. (1987) have suggested that lifestyle is more important than either body size or phyletic affinity in determining-skeletal scaling. If so, an alternative scaling of the skeleton may be demonstrated by an insect with a locomotor mechanism distinctly different from that of pedestrians such as cockroaches and giraffes. The jump of Schistocerca gregaria is a well-documented mechanical behaviour (Heitler, 1974; Bennet-Clark, 1975; Alexander, 1983) and, therefore, provides a good contextual framework in which to place an analysis of scaling. The films of Brown (1963), analyzed by Alexander (1983), indicate that during the jump impulse of the adult locust the primary loading regime in the metathoracic tibiae is bending. We have, therefore,
investigated the bending behaviour of limb segments to determine the scaling of mechanical properties. This study will show that the external skeletal morphology predicts mechanical behaviour dramatically different from the observed mechanical behaviour. It will also attempt to explain how the mechanical result may be arrived at in spite of the morphological design programme.

Materials and methods

Animal husbandry

Animals were sampled daily from a breeding colony of African desert locusts (Schistocerca gregaria Forskål) maintained at the Department of Zoology at the University of British Columbia. The animals were kept at a constant temperature of 27°C, at a humidity of 56%, with a photoperiod of 13 h:11 h (L:D) and fed a diet of head lettuce and bran. A sample of five individuals was collected each day beginning on the first day following emergence from the egg until approximately sexual maturity (approx. 35 days). Each animal contributed both left- and right-side meta- and mesothoracic tibiae, resulting in four samples from each individual. Replicates were performed to increase precision over the first seven and final 15 days of sampling. There was no significant heterogeneity between replicates for a given day, so all replicates were pooled. As a result, there are different sample sizes across the time series of morphological and mechanical measurements.

Animals were decapitated and weighed immediately to the nearest 0.1 mg. All of the morphological and mechanical measurements were then performed in air on tibial segments within 10 min of removal from the animal. Control experiments indicated that exposure to air for this short period did not alter the mechanical properties significantly.

Morphological measurements

The length and diameter of the tibial segments of both the mesothoracic and metathoracic tibiae were measured either with a filar micrometer eyepiece (Wild 15XSK) attached to a dissecting microscope (Wild M5) or, where the tibia length exceeded the length of the micrometer’s graticule (the fifth instar and adult tibia lengths), with a vernier calliper. Micrometer measurements were made to the nearest 10 μm and calliper measurements to the nearest 20 μm. Morphological landmarks were defined to provide ease of location and to indicate the dimensions of uniform limb segments. That is to say, geometrically complex morphological features associated with the joint articulations were excluded from linear measurement. In the case of the mesothoracic leg, the tibial length was defined as the length measured on the lateral surface from a point approximately level with the femoro-tibial articulation to the tibio-tarsal articulation. The metathoracic tibial length was defined as the distance between the depression in the posterior surface of the tibia just distal to the knee joint articulation, at the maximal extent of sclerotized tibial cuticle, down the posterior of the tibia to a point opposite the insertion of the first movable spine at the tibio-tarsal joint. Diameters were
Mechanical scaling in locust legs

Fig. 1. Diagram showing the anatomical landmarks used in measuring length and diameter of the tibiae. The metathoracic tibia is on the left and mesothoracic tibia is on the right. Diameters were measured at the mid-length point. \( L \), tibial length; \( D \), tibial diameter. The values of \( L \) and \( D \) vary between instars (see Fig. 4).

determined to be the largest diameter of the semi-elliptical cross section at the mid-shaft point (Fig. 1).

Dynamic mechanical measurements

After morphological measurement, each metathoracic tibia was placed in a mechanical testing frame that imposed a three-point load with a dynamic, or time-variant, deformation. The theoretical and practical development of this dynamic testing technique has been reported previously (DeMont and Gosline, 1988; Lillie and Gosline, 1990). Therefore, only the principles and an outline of modifications made to generate three-point bending will be described. The device consists of an actuator that delivers the time-variant displacement, monitored by a displacement transducer, and a force transducer that measures the resultant force developed across the test piece (i.e. a metathoracic tibia) at the two ends of the sample (Fig. 2).

The actuator consisted of a length of 3.759 mm o.d. stainless-steel hypodermic tubing attached at one end from an electromagnetic vibrator (model V203, Ling Dynamic Systems, Royston, Hertfordshire, UK) and stepped down at the other end to an 18 gauge hypodermic needle. The end of the needle was cut off flush and polished smooth. Out of its end protruded a length of 3.6 kg nylon fishing leader.
The nylon loop was adjustable and could be shortened to hold the midshaft of a test piece flush against the end of the actuator by turning a 4-40 machine screw, which 'spooled' up the slack nylon.

The free ends of the test piece were pulled upwards against the ends of a window cut in the side wall of a length of 3.759 mm o.d. stainless-steel tubing. The tubular holder was attached to a force transducer with a 2-56 stainless-steel machine screw. The size of the window was scaled to provide a ratio of approximately 10:1 of test piece total working length to diameter to maintain a relatively consistent relationship of bending to shearing moments in the test pieces. In order to maintain this ratio in legs of different sizes, several holders were made with appropriately sized windows. The ratio was deemed a reasonable compromise between the wish to introduce primarily a bending moment with respect to shearing moments and the difficulties of fabricating small holders. The force developed across the test piece was measured with a cantilever-like transducer fabricated out of 0.381 mm thick stainless-steel shim stock. This material provided appropriately small deflections (less than 1% of the imposed displacements). Semiconductor strain gauges (type SR4 SBP3-20-35, BLH Electronics, Canton
MA) were bonded on both surfaces of the cantilever. Semiconductor gauges provided appropriate sensitivity of 0.0473 N V⁻¹. The resonant frequency of the transducer was 1.40 kHz with the smallest holder, 0.95 kHz with the largest and 0.65 kHz for the ensemble apparatus.

As described previously (DeMont and Gosline, 1988), the electromagnetic vibrator was driven by the noise generator of a spectrum analyzer (model 5820A, cross channel spectrum analyzer, Wavetek Rockland Inc., NJ), which provided a constant power spectrum over the range of frequencies collected (0–200 Hz). At each frequency, the spectrum analyzer calculated both the ratio of the amplitudes of the Fourier components of the force and displacement transducer outputs and the phase shift (δ) between the two signals. Spectra were collected from 0 to 200 Hz, and approximately 256 spectra were averaged to produce one spectrum per test piece. The flexural stiffness (EI) of the specimen at each frequency was calculated using the following relationship for static three-point bending:

$$EI = \frac{Fx^3}{48d},$$

where x is the length of the test piece (i.e. the length of the window in the tubular holder), F is the developed force and d is the deflection at the mid-point of the beam (rearranged from Gordon, 1978). EI is composed of E, the tensile stiffness of the beam’s material, and I, the beam’s second moment of area. In these experiments the calibrated amplitudes of the Fourier components of the force and displacement transducer outputs were employed as F and d in equation 1 to produce a complex flexural stiffness (E*I) (adapted from Ferry, 1980).

E'I, the storage flexural stiffness, a measure of the energy stored elastically per loading cycle, can be found by calculating the in-phase component of the complex flexural stiffness as follows:

$$E'I = E*I\cos\delta.$$  (2)

The energy loss flexural stiffness (E'I) is the out-of-phase component of the complex flexural stiffness:

$$E'I = E*I\sin\delta$$  (3)

and is a measure of the energy dissipated per loading cycle. The tangent of the phase shift (tanδ=E'I/E'I) can be used calculate the percent resilience per half-cycle (R) of the structure as follows:

$$R = (e^{-\pi tan\delta})100$$  (4)

(Wainwright et al. 1976). Explicitly, R is the ratio of the energy recovered elastically to the energy input to the test piece in each loading cycle. All of these calculations were performed on a Digital Equipment Corporation MINC-11/23 computer.

Statistics

Except where noted, statistical tests were chosen based on criteria presented in Sokal and Rohlf (1981). Owing to the non-zero variance associated with the
morphometric variables measured in this study, all regressions were model II regressions (Sokal and Rohlf, 1981). All statistical tests were performed with the STATGRAPHICS (STSC, MA) statistical software package.

Results

Ontogenetic accumulations of body mass followed a characteristic sigmoid curve adequately described by the von Bertalanffy growth function (Pitcher and Hart, 1982). Fig. 3 shows the daily means of body mass as well as the fitted curve. The values of sample size for each day are the same for Figs 3 and 4. Body mass ranged from 0.0109 g for first-day, first instars to 3.541 g in adult, sexually mature females. The data show that mass accumulates in a relatively continuous manner within each instar. Adult locusts continued to accumulate mass for the first 4–7 days after molting and then leveled off at their equilibrium mass. The assumption of the von Bertalanffy growth function, that the individual will grow in a logarithmic way up to a point where ingested calories are diverted from general somatic growth to reproductive growth, seems reasonable in this case as growth leveled off at approximately sexual maturity (about day 30).

Fig. 3. The relationship of body mass to the age of the locust. Data are reported as means and standard errors of the mean. The regression is fitted to the von Bertalanffy relationship with the following form: mass=4.027(1−e^(-0.045x))^3, where x is age in days (F_8=987.8; d.f.=2,33; r^2=0.962). Numbers indicate the sample sizes for each day. Asterisks indicate data from individuals on the first day following a molting.
All allometric relationships reported here proved to be significant to the 0.05 probability level. A significant sexual dimorphism develops in adults, with the females having approximately 50% more mass than the males (ANOVA, $F_s=21.969$, d.f. =1,192, $P>0.05$). Analysis of covariance (ANCOVA) indicated no significant effect of sex, beyond the effect of mass, on any of the morphological or mechanical variables measured (ANCOVA, $F_s=2.451$ for mesothoracic tibia diameter on body mass was the relationship most closely approaching significance, d.f. =1,378). Therefore, data from both sexes were pooled in each regression.

**Morphology**

Fig. 4 shows the change in tibial length (Fig. 4A) and diameter (Fig. 4B) with increasing age. Analysis of variance (ANOVA) indicates significant heterogeneity between groups, and Newman–Keuls multiple-range tests indicate that each instar is a homogeneous, independent group. This confirms that the sample values from the population are reflecting what we believe to be occurring in individuals and that the external dimensions of leg length and diameter are not changing within instars. Analysis of variance of residuals indicated that tibial length and diameter were independent of body mass within each instar, biasing the overall allometric relationships of length and diameter against body mass (Draper and Smith, 1981). Therefore, all values for body mass and tibial length and diameter within each instar were pooled, and a mean value for each variable for each instar was used in the allometric regressions. These data also indicate that within each instar the metathoracic legs are approximately twice as long as the mesothoracic legs, while having approximately the same diameters.

Figs 5 and 6 show the log-transformed plots of leg length and diameter against body mass. Metathoracic tibial lengths followed the relationship of body mass raised to the 0.38 power (s.e. =0.01, $r^2=0.996$), while mesothoracic tibial lengths scaled to mass to the 0.36 power (s.e. =0.01, $r^2=0.995$) (Fig. 5). Metathoracic tibial diameter scaled to body mass to the 0.31 power (s.e. =0.01, $r^2=0.996$), and mesothoracic diameter scaled to the 0.28 power (s.e. =0.01, $r^2=0.996$) (Fig. 6). This indicates that, as the animal grows, the limb segments are getting relatively longer and more spindly rather than maintaining a constant proportion of length to diameter, as predicted by geometric similarity (GSM), or becoming stouter, as predicted by distorting allometries (i.e. ESM or CSSM). In each case, the slopes of the allometric relationships between the leg dimensions and body mass were not statistically distinguishable between the metathoracic and mesothoracic legs.

A convenient index for comparison is the allometric relationship between tibial length and diameter. The distorting allometries (i.e. ESM and CSSM) predict that lengths will scale to diameters raised to a power less than one, resulting in increasing stoutness. Geometric similarity predicts an exponent of exactly 1.0 or isometry. Locust tibial lengths, however, scale to diameter raised to a power greater than one (1.21, s.e. =0.01, $r^2=0.999$ for metathoracic legs and 1.25, s.e. =0.01, $r^2=0.999$ for mesothoracic legs, Fig. 7). These exponents are signifi-
Fig. 4. (A) Plot of tibial lengths for mesothoracic (○) and metathoracic (□) legs with increasing age, showing discontinuous growth across instars. Individual points represent means and 95% confidence intervals to show the similarities within, and differences between, instars. (B) Plot of tibial diameters with increasing age. The symbols are the same as in Fig. 4A. For values of N, see Fig. 3.

...cantly higher ($P<0.01$ in both cases) than any existing allometric model predictions. Thus, the tibiae in Schistocerca gregaria scale in a manner that is not only different in value from the existing models but in direction as well. As was the case
above, the slopes of the allometric relationships for leg morphology were statistically indistinguishable between the metathoracic and mesothoracic legs.

Mechanical measurements

Fig. 8 shows a representative spectrum of storage and loss stiffness values across the sampled frequency span. There appears to be virtually no frequency dependence of the data. The deviation of the relationship between both storage and loss stiffness and frequency from a slope of zero is significant, but only results in a 6.4% change in actual storage stiffness per decade change in frequency. Results reported by Bennet-Clark (1975) indicated that the jump impulse duration is approximately 25–30 ms. Although the impulse is a transient event and, therefore, difficult to correlate with steady-state vibration (\textit{vis à vis} a biologically relevant strain rate), we decided to use the impulse duration as a measure of the half-cycle period and use 22.5 Hz (i.e. a five-point average between 20 and 25 Hz) as our reference frequency for comparison between samples. The relatively larger scatter of the energy loss data ($E''t$) is due to its dependence on what is, in this case, the sine of a small angle (equation 3), whereas the energy storage stiffness ($E'f$) depends on the cosine of a small angle and is smoother (equation 2). The
approximately 30-fold difference in energy and loss terms results in a resilience of 91% for this data set.

The time course of changes in the flexural stiffness ($E'$) of the metathoracic tibiae describes a series of asymptotic curves, where the stiffness is relatively low immediately after a moult and increases within the next 24–48 h by approximately an order of magnitude (Fig. 9). This seems to be a reasonable consequence of the protein cross-linking and cuticle dehydration that occurs during this period (Neville, 1975; Vincent, 1980). The lack of an appreciable decrement in stiffness on the first day of the third instar may reflect an uncertainty in ageing the insects (± half a day) at a point where the stiffness is changing rapidly, rather than a fundamental difference in the cuticle's behaviour at that point.

The observation that the stiffness of the tibiae is relatively low immediately after moulting suggested that it might be prudent to create a separate data set for allometric analysis that excluded all stiffness values from individuals on the first day post-moult, thereby preventing the analysis of the overall scaling programme from being biased by the transient physiological events of cuticle stiffening in moulting. Flexural storage stiffness scaled to body mass raised to the 1.59 power
Mechanical scaling in locust legs

Fig. 7. The relationship of the logarithm of tibial length (mm) and the logarithm of tibial diameter (mm) for mesothoracic (□) and metathoracic (□) legs. Individual points represent means and standard errors for each variable for each instar. The equation of the regression for the mesothoracic legs is \( y = 0.961 + 1.252x \) (\( F_s = 12537.4; \) d.f. = 1, 4; \( r^2 = 0.9997 \)). The equation of the line for the metathoracic legs is \( y = 1.234 + 1.212x \) (\( F_s = 35038.2; \) d.f. = 1, 4; \( r^2 = 0.9999 \)). The dashed lines are the 95% confidence limits of the regression lines.

(s.e. = 0.02, \( r^2 = 0.937 \)) for all data, and to the 1.53 power (s.e. = 0.02, \( r^2 = 0.954 \)) for the data without individuals in the first day of an instar (Fig. 10). We regard the latter value as characteristic of functionally equivalent states in the population (see Discussion) and appropriate for scaling comparisons.

A full series of mechanical measurements was not made on the mesothoracic tibiae, but morphological measurements indicated that within each instar they had virtually the same diameters as the metathoracic tibiae. Thus, one may expect that mesothoracic tibiae will exhibit the same flexural stiffness as metathoracic tibiae. Mechanical analysis of test pieces of equal lengths of metathoracic and mesothoracic tibia from five 35-day-old adults showed this to be the case. There was no statistical difference in the mean flexural stiffnesses (\( t_s = 0.9918 < t_{0.05[4]} = 2.776 \)).

The time course of resilience, shown in Fig. 11, demonstrates that resilience values also increase asymptotically from local minima on the first day of each instar and achieve higher values over time. Significant differences do exist among means across the entire life history (ANOVA of arcsine-transformed resiliences, \( F_s = 15.928; \) d.f. = 34, 460). However, it is impossible to say whether this represents a real change in mechanical properties or whether the smaller, more difficult to handle, specimens have a greater variance and, therefore, a lower mean due to the
Fig. 8. Mechanical test data showing the logarithm of flexural storage stiffness ($E'/I$, N m$^2$) and the loss stiffness ($E''/I$, N m$^2$) against the logarithm of frequency (Hz) of the imposed deformation for an adult locust of 34 days of age along with their regressions. The equation of the regression for the energy storage stiffness is $y = -3.948 + 0.026x$ ($F_s = 217.7; \text{d.f.} = 1,67; r^2 = 0.7646$). The equation of the regression for the energy loss stiffness is $y = -6.238 - 0.085x$ ($F_s = 19.682; \text{d.f.} = 1,67; r^2 = 0.2271$). The dashed lines are the 95% confidence limits for the regression line for $E'/I$.

potentially truncated distribution of resilience values (i.e. resilience cannot be greater than 100%). It is interesting that the mechanical resilience values for the adults approach an average value of 93%. This is very similar to the values of 93% for sheep plantaris tendon (Ker, 1981), 97% for locust resilin (Jensen and Weis-Fogh, 1962) and 91% for the most resilient synthetic rubbers (Ferry, 1980).

Discussion

The scaling of *Schistocerca gregaria* tibiae results in relatively longer and spindlier skeletal elements, while existing allometric models predict, at the least, isometry if not distortions away from increasing spindliness and towards stoutness. This empirical scaling relationship deviates both from theoretical predictions (McMahon, 1973, 1984; Bertram and Biewener, 1990) and from some empirical observations (McMahon, 1975; Prange, 1977; Bertram and Biewener, 1990). However, it is in very close agreement with Carrier's (1983) observations on the ontogenetic scaling of limb bones in the jack rabbit, *Lepus californicus*. The nature of the existing allometries that predict distortions of morphology is that when beams are longer than a critical length, with respect to their diameter and their...
material properties, they will either buckle and fail or will deform to a degree that is incompatible with the function of the skeletal system. In the literature it is generally assumed that design strategies must increase the mechanical stiffness of skeletal support structures, presumably by changes in morphology that increase the amount of load-bearing material, to compensate for increases in the mass of the structure (e.g. ESM or CSSM). Indeed, in one case where limb bones became relatively more slender in ontogeny, producing a potentially more deformable structure, there was an observed increase in material stiffness of an order of magnitude (Carrier, 1983). This makes it important, in the context of locust tibial scaling, to determine what actually happens to the mechanical properties of the leg because the observed morphology predicts that the legs are becoming relatively more deformable as the animals grow.

The various scaling models can be used to predict how the flexural stiffness could scale with increasing body mass. The flexural stiffness has two components: $E$, the tensile modulus of the material from which the beam is made; and $I$, the second moment of area, a measure of the distribution of material across the beam’s cross section. For now we may assume that small locusts and large locusts are made of the same material, so that $E$ is a constant (Hepburn and Joffe, 1974b), and that changes in $EI$ reflect changes in $I$, which we can relate to morphology. For tubes of circular cross section, $I$ is proportional to diameter raised to the fourth
Fig. 10. The relationship of the logarithm of the flexural storage stiffness (N m²) and the logarithm of body mass (g). Each point is the result of one mechanical test like that shown in Fig. 8. These data exclude points collected from individuals on the first day after each moult. The equation for the regression is $y = -4.566 + 1.532x$ ($F_1 = 7637.8$; d.f. = 1,426; $r^2 = 0.9442$).

power. Although locust tibiae and vertebrate long bones do not have strictly circular cross sections, we will assume cylindrical geometry, making $l$ proportional to diameter to the fourth power. Given these assumptions, we can use equation 1, and allometric predictions, to anticipate how $EI$ might relate to body mass. For GSM, diameter ($D$) scales to mass to the one-third power and prediction of $EI$ follows thus:

$$D \propto \text{mass}^{0.333},$$

so

$$l \propto (\text{mass}^{0.333})^4$$

or

$$l \propto \text{mass}^{1.333}.$$ 

Geometric similarity, therefore, predicts that $EI$ should scale to body mass raised to the 1.33 power. Using a similar process, elastic similarity predicts an exponent of 1.50 and constant stress similarity predicts an exponent of 1.60.

If one makes this same calculation using the morphological allometric relationships for the external dimensions reported here for the locust, and makes the same assumptions about $EI$, one predicts that $EI$ in locusts should scale to body
mass to the 1.244 power. This was not the case. The observed exponent for $E'/l$ as a function of body mass incorporating the complete data set was not significantly different from the prediction of constant stress similarity (slope or $b=1.59$, $t_s=0.498$, d.f. = 507). The exponent for the data set excluding individuals from the first day of the instar was marginally different from the prediction made by elastic similarity ($b=1.53$, $t_s=2.329$, d.f. = 419). Both data sets were different from the prediction of an exponent of 1.244. Therefore, in spite of a morphological programme that deviates from any expectation, the mechanical properties scale in a way that is consistent with existing models. This indicates that measurement of external dimensions alone does not provide sufficient information to determine the mechanical behaviour of the skeleton in this case. This observation poses two questions: (1) what is compensating for the morphological programme that allows the mechanics to achieve a mechanically reasonable result, and (2) what is the design ‘strategy’ responding to in producing the observed unanticipated scaling programme?

With respect to compensation, it is possible that the modulus of the cuticle material is altered to accommodate changes in morphology of the limb segment in order to maintain an elastically similar flexural stiffness. Certainly, the modulus increases during the immediate post-moult period of scleritization as a result of dehydration (Hepburn and Joffe, 1974a; Vincent and Hillerton, 1979; Vincent, 1980). Indeed, it may be that the material properties of the cuticle are different at

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**Fig. 11.** The time course of change in resilience of the metathoracic tibia with age. Data are reported as mean values and 95% confidence limit for each day. Data from individuals on the first day following a moult are denoted by asterisks. Numbers indicate the sample size for each day.
Hepburn and Joffe (1974b) have suggested, however, that the cuticle of *Locusta migratoria* maintains a similar stiffness in tanned fifth instar and adult femoral cuticle. They suggest that the ratio of stiffness to mass is a constant for tanned cuticle across instars and that this is a response to a constant ratio of load developed in a jump to body mass across the instars (Hepburn and Joffe, 1974b). If the tanned cuticle of *Schistocerca gregaria* has the same modulus regardless of age, then the design strategy that results in increasingly spindly legs in locusts must be fundamentally different from that observed for *Lepus californicus*.

It is also possible that the distribution of cuticle material changes across instars, resulting in a change in $I$ that is not reflected in a change in the externally measured diameter. The formula for $I$ is:

$$I = \int_0^{y_{max}} y^2 dA,$$  \hspace{1cm} (5)

where $dA$ is the increment of cross-sectional area located a distance $y$ away from the neutral axis, a line through the centre of mass of the cross section normal to the bending moment (Gordon, 1978). The importance of this relationship is that material away from the neutral axis contributes greatly to the stiffness of the test piece. Because the cuticular segments of locusts are thin-walled cylinders, a small adjustment in the distribution of material on the inside of the cross section of a locust leg could impart large changes in mechanical properties that are not easily inferred from measurement of external dimensions. Such a sensitivity to changes in internal material distribution is not necessarily present in the thick-walled bones of terrestrial vertebrates. Certainly, endocuticle is added after moulting within each instar (Neville, 1975), although it is not clear if material is added in a manner that would alter the relationship between the leg diameter and $I$. It is also not clear that accumulations of endocuticle contribute to changes in the mechanical properties of the tibiae. At apolysis (approximately 1–2 days before moulting, Queathum, 1991) there is a reorganization of the endocuticular material that involves an enzymatic digestion of the endocuticle (Zacharuk, 1976), presumably decreasing the second moment of area. We observe no decrement in flexural stiffness within any instar that can be correlated with the occurrence of apolysis (Fig. 9).

The accumulation of endocuticle also does not explain how changes might be mediated across instars. Gabriel (1985b) reported that the metathoracic tibia’s cuticle thickness in the anterior direction relative to the lateral direction maintains a constant proportion across the juvenile instars, but increases by 50% in adults. This differential thickening could contribute to changes in $I$ that are not reflected in external diameter. However, it is not known to what extent endocuticle accumulation is responsible for the increased wall thickness seen in adults, or why the discontinuity in wall thickness between all the juvenile instars and the adults is not reflected in the flexural stiffness. What Gabriel’s data do suggest is that, if $I$ is being adjusted to maintain the observed relationship between $E’I$ and body mass,
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It is not, in juvenile instars at least, being accomplished with simple changes in wall thickness. Rather, there are probably changes in cross-sectional shape that are producing changes in $I$.

At present we are unable to resolve the extent to which either $E$ or $I$ or both are being modulated to produce the observed mechanical scaling. We are also unable to discriminate definitely the mechanical role of the endocuticle, either within or across instars. However, we should be able to resolve the nature of the stiffness or shape changes in the tibia when we have sectioned the tibiae used to collect the mechanical measurements and determined $I$ for their endocuticular and exocuticular components.

Exoskeletal vs endoskeletal design

The sensitivity of $I$ in thin-walled exoskeletal systems to changes in wall morphology suggests a fundamental difference in the use of exo- and endoskeletal designs. Currey (1980, 1984) has generated a model that predicts the optimal inner to outer diameter ratio ($k$) for a hollow bone. The model plays off the increases in $I$ per unit mass that comes from using ever larger diameter, ever thinner, tubular skeletal members against the penalty of having to carry around the mass of the non-structural material inside the tube, such as marrow or fat. The analysis predicted different values for $k$ based on the variable that the design programme optimized, such as mass-specific strength or stiffness. For a selection of terrestrial vertebrate long bones the model seemed to anticipate effectively the relatively thick-walled tubing as an adaptation to resist failure from impact loading (Currey, 1984). A notable exception is the air-filled bones of birds, where the walls are relatively thin, in comparison to the marrow-filled bones of terrestrial mammals (Currey, 1984). Fig. 12 shows the ratio of total mass of bone and luminal contents to the mass of a solid bone with the same value of $I$, for various $k$ ratios. An important feature of Currey’s model is that the relative density of marrow is about half that of bone, i.e. the density ratio ($\rho$) is 0.50. In Schistocerca gregaria the $\rho$ of the haemolymph to the cuticle material is about 0.88 (Wainwright et al. 1976). For the locust, the minimum that occurs at about $k=0.35$ represents a less than 1% savings in mass over a solid rod morphology (Fig. 12). Measurements from the cross section of the metathoracic tibial segment in a 10-day-old adult Schistocerca gregaria from Jensen and Weis-Fogh (1962) show that $k=0.92$, indicating that this skeletal member is not approaching the optimum associated with a minimum mass.

The fact that insects do not have skeletons made from thick-walled tubing may indicate that minimizing the mass of non-structural material is not the over-riding design strategy. In exoskeletal animals, where the material on the inside of the tubing is the muscle and circulatory fluid, the added weight of this material may not represent the same penalty as marrow or fat does in vertebrates. If it is the locust’s strategy to maximize its internal volume, then Fig. 12 predicts a thin-walled morphology that achieves large volume and is limited only by buckling (Currey, 1980). The dashed vertical line in Fig. 12 originating at $k=0.96$ indicates
Fig. 12. Theoretical model of optimal internal to external diameter ratio ($k$) for hollow skeletal structures with various ratios of lumenal content to wall material relative density ($\bar{\rho}$). The line $\bar{\rho}=0.88$ is the condition that exists in Schistocerca gregaria, which has a slight minimum at $k=0.35$. For $\bar{\rho}=0.0$, which approximates the air-filled bones of birds, the model predicts thin-walled tubes limited by buckling. As one moves to relatively less dense tubing material, the minima become shallower and predict thicker walls. $\bar{\rho}=0.5$ is the condition describing bone (Currey, 1980, 1984), which has a shallow optimum at approximately $k=0.7$. At $\bar{\rho}=0.13$ (steel tubing filled with an aqueous medium) there is a deep minimum at $k=0.93$, with a weight savings of about 51%. The boundary condition of equal relative densities for the tubing and the inside contents ($\bar{\rho}=1.00$) predicts that the minimal mass solution occurs in solid rods rather than hollow tubes. The dashed vertical line originating at $k=0.96$ is the limit to $k$ imposed by unstable buckling based on data for the material properties of locust cuticle (Vincent, 1980) and the analysis of buckling of Currey (1980). This represents the ultimate limit to being thin-walled.

The similarity of the observed $k$ ratio and the buckling limit would seem to support the idea that the design in locusts maximizes internal volume.

Scaling in cursorial and jumping insects

The observation that locusts' limb morphology deviates from the existing allometries while that of other exoskeletal animals, such as cockroaches and
spiders, does not (Prange, 1977), would seem to indicate that the exoskeletal body plan does not in itself determine the scaling of limb dimensions. That is, the exoskeletal design may have allowed this option, but evolution has not demanded that all such designs follow it. Therefore, it would seem reasonable to suggest that the design programme that produces the morphological scaling in *Schistocerca gregaria* represents an adaptation for some specific functional attribute. We suggest that the kinematic and energetic demands of jumping in growing animals may be met more effectively by the allometry seen in the locust, rather than the geometrically similar growth pattern seen in cursorial animals such as the cockroach.

If it is true that the morphology of the metathoracic legs is demonstrating a specialization for jumping, then we might hypothesize that the pro- and mesothoracic legs (i.e. 'walking legs') would scale in a manner different to the metathoracic leg ('jumping leg'), but this is not the case. It has been noted that prothoracic legs appear to follow isometry (Gabriel, 1985a); however, the data on mesothoracic legs clearly show a similar developmental programme to that for the metathoracic legs. While maintaining the same scaling relationship to body mass across ontogeny, the metathoracic tibiae are twice the length of the mesothoracic tibiae. The third power dependence of deflection of a loaded beam on length (equation 1) predicts, therefore, that the metathoracic tibiae are eight times more deflectable than the mesothoracic tibiae, given the same flexural stiffness. Since equal lengths of mesothoracic and metathoracic tibia have the same flexural stiffness in adults, it seems reasonable to assume that the interleg similarity in stiffness per unit length would be maintained across ontogeny. Further, the peak loads during jumping are approximately 20 times the force of gravity (Bennet-Clark, 1975) and are distributed over only two jumping legs, whereas the loads of standing or walking (approximately 1 × the acceleration of gravity, g) are distributed over six legs. The walking tibiae, then, may experience several hundred times less bending deflection in walking than do the metathoracic legs during jumping. Even in the case where a locust lands on a single mesothoracic leg at the end of a jump, the kinetic energy would be absorbed by a single leg with one-eighth of the compliance of each metathoracic leg. In this extreme case, the mesothoracic leg would still experience four times less deflection than a metathoracic tibia. Even though the mesothoracic tibiae are probably not experiencing exclusively a bending load, this analysis indicates that they are distinctly overbuilt. Thus, the genetic constraint on the development of metameristic, morphological characters may limit the ability of natural selection to minimise the amount of extra material the animal carries around. It may turn out that the genetic mechanisms that control metathoracic leg development are linked functionally to the genetic control of mesothoracic legs and even perhaps to appendages on other segments of the body. Interactions across body segments, with respect to the control of expression of metameristic characters, have been seen in the bithorax gene complex in *Drosophila melanogaster* (Lewis, 1978). Since jump performance, in terms of take-off velocity, is inversely dependent on body mass (Bennet-Clark,
1977), there would seem to be a benefit in keeping excess weight to a minimum. If so, then the over-design of the mesothoracic legs may represent a penalty to be paid for the sake of having jumping legs that perform well and of having a genetic control mechanism that is not specific to a single body segment. It may prove interesting to test this hypothesis by examining the scaling of antennae or mouth parts of the locust to determine the extent of this interaction.

**Ontogenetic vs phylogenetic scaling**

In this study we have used ontogeny as a model for the effect of body mass on the morphological and mechanical design of the limb skeleton of *Schistocerca gregaria*. We find a developmental programme that results in increasingly spindly legs, suggesting more easily deformable beams, but the mechanical properties are adjusted to produce elastically similar tibiae. We believe that this provides information about the mechanical design of jumping animals, but is ontogeny a justifiable model for the effect of body size? Is it fair to assert that the ontogenetic scaling observed in locusts demonstrates mechanical design principles? If it is, then we would expect to find similar scaling in other jumping animals.

It seems significant that the morphological scaling relationship reported here, while different from phylogenetic comparisons, is very similar to the ontogenetic morphological changes seen in the jack rabbit (i.e. tibia length is proportional to tibia diameter$^{1.21}$ for locust, tibia length is proportional to tibia diameter$^{1.30}$ for *Lepus californicus*, Carrier, 1983). Also interesting is Carrier's observation that material stiffness and the second moment of area of the metatarsal bones increase with the first power of body mass. This indicates that the flexural stiffness is increasing with the second power of body mass, faster even than the exponent of 1.53 observed for locusts.

It is tempting to suggest that the similarity in *Schistocerca gregaria* and *Lepus californicus* ontogenetic scaling is demonstrating a developmental strategy that is adopted generally by jumping animals. However, there is an important difference in the development of locusts and jack rabbits that points to a potential danger in using ontogenetic observations to examine the effect of body size. This distinction lies in comparing animals that are not functionally similar. Both adult locusts and adult jack rabbits hop or leap as their mode of locomotion, but whereas juvenile locusts hop (Gabriel, 1985a), juvenile jack rabbits prefer not to (Carrier, 1983). Carrier (1983) has reported that neonate jack rabbits (<300g) are 'unsteady' locomotory performers, relying on crypsis to avoid predation. Once over 600g, however, they develop good locomotor performance and readily resort to jumping when startled. Whatever the pressure that has resulted in the developmental programme in jack rabbits, it is not the need to be a functionally adequate jumper over the entire ontogenetic range of body size. A jack rabbit achieves high locomotor performance over only the final fourfold range in body mass, while the locust achieves high performance, in terms of distance covered, at points within each instar over a 200-fold range in mass (Gabriel, 1985a). Interestingly, locusts start each instar as poor jumpers (Gabriel, 1985a; Queathum, 1991) with relatively
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Over the following 24–48 h the cuticle stiffens by approximately an order of magnitude and locomotor performance improves. Thus, it appears that locusts go through developmental changes within each instar that are similar to those that the rabbit goes through over its entire lifetime. In a sense, the rabbit’s development is composed of a single ‘instar’, while the locust’s development is composed of functionally competent individuals that come in six different sizes. Since the individuals of each instar over 24 h old represent functionally similar locusts of different sizes, we feel confident that the scaling relationships reported here provide important insights into the design of jumping animals.

Design of tibiae for jumping

It is appropriate, therefore, to attempt to explain the observed skeletal scaling in the context of the locust’s locomotor strategy. The increasing slenderness of the tibiae may be a response to falling accelerations produced in the jumps of large animals compared to the jumps of small ones. If larger locusts produce less acceleration than small ones, then their longer limbs may be an adaptation to increase the time that their feet are able to do work on the ground. As Bennet-Clark (1977) points out, as animals get bigger their acceleration in jumping decreases, so that dynamic loading in jumping is decreasing at the same time that the relatively static loads related to body mass are increasing. Adult locusts of 3.5 g body mass produce approximately 20 g of acceleration (Bennet-Clark, 1975), while adult fleas (Spylopsyllus cuniculus) of 0.45 mg produce accelerations of over 135 g (Bennet-Clark and Lucey, 1967). Locust tibial morphology may be following a programme designed to accommodate declining accelerations encountered with increasing body mass, rather than body mass per se. Therefore, scaling relationships that attempt to explain the mechanical design programme relating morphology and body mass make predictions in a direction opposite to that seen in locusts. Counter to this argument, however, Scott and Hepburn (1976) have suggested that small locusts do not produce larger accelerations than adults. They report a constant relationship of approximately 10 g of acceleration in several African grasshoppers, as well as through the ontogenetic sequence of Locusta migratoria. None of their observations seems to be as large as the 20 g reported by Bennet-Clark (1977) for adult Schistocerca gregaria. It would, therefore, be of value to know explicitly how the accelerations developed during the jump change from small to large locusts.

An alternative explanation for the morphological programme may lie in a reinterpretation of the function of the exoskeleton. Schmidt-Nielsen (1984) suggests that skeletons are rigid structures that act either as support beams or as lever arms to be acted on by muscles to provide movement. Two observations in this study indicate that perhaps the locust tibial skeleton is acting not so much like a rigid lever arm, but rather as an elastic energy storage device. From equation 1 and a peak acceleration of 20 g (see above), the ground reaction force for a 0.003 kg adult locust will produce a deflection at the end of the tibia of the order of 3 mm, or about 13 % of the tibia length. In fact, Brown (1963) has stated that some of his
high-speed films show the tibiae bending during jumps. The energy required to deform a linear spring is equal to half of the product of the deformation and the force applied, which in this case is 1.2 mJ of energy for both legs together. If we incorporate a cuticular resilience of 92%, then approximately 1.1 mJ of energy is returned as elastic recoil from the tibiae during the jump. Bennet-Clark (1975) has reported that an adult female *Schistocerca gregaria* requires about 11 mJ for a jump. Thus, approximately 10% of the total energy of the jump is recovered from energy stored in the tibiae. The relative increase in tibial spindliness with increasing size may represent an attempt to create a more deflectable beam and, therefore, a larger-capacity energy reservoir, as the peak accelerations are falling during ontogeny. Additionally, the high resilience values of 90–93% for tibial cuticle (Fig. 10) indicate that the material's properties are well matched to an energy storage function.

These observations suggest that it is more appropriate to think of locust tibiae as bending springs rather than simple rigid levers. This use of energy storage seems significantly different from that of other systems previously examined in that it does not act as a momentum collector, capturing kinetic energy from a muscular contraction in a previous stride as potential spring energy to be recovered as kinetic energy in the following stride. Instead, the spring energy is stored and recovered in the same stride, not unlike the model proposed for primary flight feathers in pigeons (Pennycuick and Lock, 1976). Why store it when mechanical hysteresis will only decrease the amount of muscular energy that does any useful work in locomotion? It may turn out that the energy stored in the tibia early in the force impulse in the jump is stored at a time when the mechanical advantage of the muscle–apodeme–tibia lever system is high, but the ability of the locomotor system to do work on the ground is low, and energy can be stored in the spring. That energy could then be returned later within the same loading event when the mechanical advantage of the muscle–apodeme–tibia lever system is low (Bennet-Clark, 1975), but the ability to do work is high. A useful metaphor for this type of design may be an archer's compound bow where eccentric cams alter the mechanical advantage of the bow on the arrow. When a loaded compound bow is released, the force continues to rise as the arrow accelerates, producing higher velocities and longer distances than a traditional bow where the force falls as the arrow is accelerated. It may prove that the tibial springs are utilizing changes in mechanical advantage in the same manner, maximizing take-off velocity and, as a result, trajectory distance.

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