J. exp. Biol. **140**, *243–255 (1988)*
Printed in Great Britain

KANGAROO RAT LOCOMOTION: DESIGN FOR ELASTIC ENERGY STORAGE OR ACCELERATION?

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Accepted 20 April 1988

Summary

Mechanical stresses (force/cross-sectional area) acting in muscles, tendons and bones of the hindlimbs of kangaroo rats (*Dipodomys spectabilis*) were calculated during steady-speed hops and vertical jumps. Stresses were determined from both high-speed ciné films (light and X-ray) and force plate recordings, as well as from *in vivo* tendon force recordings. Stresses in each hindlimb support element during hopping (1·6–3·1 m s^{-1}) were generally only 33 % of those acting during jumping (≥40 cm height): ankle extensor muscles, 80 ± 12 (S.D.) *versus* 297 ± 42 kPa; ankle extensor tendons, 7·9 ± 1·5 *versus* 32·7 ± 4·8 MPa; tibia, −29 ± 5 *versus* −110 ± 25 MPa (all values are for hopping *versus* jumping). The magnitude of stress in each structure during these locomotor activities was similarly matched to the strength of each element, so that a consistent safety factor to failure is achieved for the hindlimb as a whole (1·5–2·0). The large stresses during jumping were correlated with a three-fold increase in ground reaction forces exerted on the ground compared with the fastest steady hopping speeds. We conclude that, for its size, the kangaroo rat has disproportionately large hindlimb muscles, tendons and bones to withstand the large forces associated with rapid acceleration to avoid predation, which limits their ability to store and recover elastic strain energy. Middle ear morphology and behavioural observations of kangaroo rats jumping vertically to avoid predation by owls and rattlesnakes support this view.

Introduction

Animals expend considerable energy performing mechanical work during locomotion. The ability of animals to reduce locomotor energy expenditure (by lowering the mechanical work that their muscles must perform) is generally believed to be selectively advantageous. Cavagna *et al.* (1977) identified two general mechanisms that terrestrial vertebrates utilize to diminish the mechanical work of locomotion: (i) more efficient transfer between kinetic energy and

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Key words: muscle, tendon, bone, stress.

potential energy of the body's centre of mass during walking ('inverted pendulum' mechanism), and (ii) elastic energy storage and recovery in elastic elements of the limb and trunk during trotting, running, hopping and galloping ('spring' mechanism). Elastic energy storage involves the transfer of kinetic and potential energy of the body when landing into strain energy, primarily by stretching the large tendons of extensor muscles of the limbs and feet (red kangaroo and wallaby, Alexander & Vernon, 1975; camel, Alexander *et al.* 1982; man, Ker *et al.* 1987; horse, A. A. Biewener, unpublished data). The stored strain energy is subsequently recovered when the tendons (and muscles) recoil at take-off. In the red kangaroo, energy savings by elastic energy storage and recovery can account for more than 50 % of the total work performed during a hop (Alexander & Vernon, 1975), reflected by a levelling off of the kangaroo's metabolic energy utilization at hopping speeds above $1{\cdot}7\,\mathrm{m\,s^{-1}}$ (Dawson & Taylor, 1973).

In an earlier study (Biewener *et al.* 1981), we compared the ability of a much smaller hopper, the kangaroo rat (*Dipodomys spectabilis*), to store and recover elastic strain energy during hopping with that of the red kangaroo and wallaby. We found only minimal strain energy storage (14 % energy recovery) in the ankle extensor tendons and muscles of these small hoppers. This was due to the low strains acting in the disproportionately large muscles and thick tendons of the kangaroo rat (for its size) compared with the much larger red kangaroo and wallaby. This finding suggested that these small animals, though highly specialized for saltatory locomotion, are 'overbuilt' for effective elastic energy savings. If the hindlimbs of the kangaroo rat are not designed well for elastic energy storage and recovery, what is the functional significance of such disproportionately large hindlimbs?

We propose that a competing factor underlying the locomotor ability of these animals is their capacity to accelerate and decelerate rapidly to escape predation. Saltatory movement by its nature is erratic and, hence, well-suited for maximizing changes in direction through rapid accelerations and decelerations of the animal's body. Large accelerations, however, will impose large stresses (force/cross-sectional area) within the skeletal elements of the limb. We believe that such large accelerations dictate increased size of hindlimb muscles, tendons and bones in this species, limiting energy savings by elastic energy storage and recovery.

We tested this idea by examining the levels of acceleration achieved by kangaroo rats during vertical jumps compared with those developed during steady-speed hopping (the condition appropriate for elastic energy storage and recovery). In addition, we compared the mechanical stresses developed in hindlimb bones, muscles and tendons during jumping *versus* hopping.

Materials and methods

Animals and force platform

The five animals (*Dipodomys spectabilis*, mean body mass 107 g) and some of the data collected in the present study are the same as those reported in our study examining indirect and direct measurements of locomotor muscle forces (Biewener *et al.* 1988). In that study we focused on the question: over what range of muscle stress does this species operate during its normal range of locomotor activity? Briefly, the animals were trained to hop down a 4 m runway with a force platform, consisting of five contiguous force plates (0·25 m × 0·25 m), located midway along its length. The central (third) force plate was divided along its length allowing separate recording of ground reaction forces exerted by each hindlimb. These plates were sensitive to forces acting in the vertical and horizontal (fore–aft) directions with less than 2 % cross-talk between directions. After correcting for cross-talk, the point of application or 'centre of pressure' of the ground reaction force acting on the foot could be determined to within ±0·5 mm accuracy from the central split plate by dividing the output of vertical force recorded at the front end of the plate by the total vertical force recorded. The details of this force platform and runway have been described previously (Heglund, 1981; Biewener *et al.* 1988). Average hopping speed was determined by the time it took the animals to break two photobeams 0·5 m apart over the force plates. The animals were also trained to jump when startled by a mild electric shock from small grids located on the surface of the central, divided force plate. Jump height was measured as the height change of the pelvis moving against a calibrated wall. In some cases, the animal cleared the jump at a height of 50 cm.

Vertical and horizontal (fore–aft) forces, together with a synchronization pulse from the camera's shutter, photocell outputs to determine velocity and force output from a tendon buckle (see below) were sampled at 1000 Hz by an A/D converter and entered into a microcomputer. The force signals were zeroed and filtered with a 100 Hz digital low-pass filter (Winter, 1979) before further analysis.

Data for ground reaction forces, muscle, tendon and bone stresses not published in our earlier study (Biewener *et al.* 1981) were also calculated from recordings of steady-speed hopping over a force plate of similar design and are included in the present study.

Kinematic analysis

In the earlier study, we made high-speed X-ray ciné film recordings (150 frames s^{-1}) of the animals passing over the force plate in lateral view. In the present study, and for all jumps, the animals were filmed with high-speed light film (200 frames s^{-1}, Photosonics 1PL camera and Angineaux zoom lens). Whereas joint locations were identified directly from the X-ray ciné films, dark ink markings made on the skin after the animals had been shaved were used to determine joint positions in the light films. The ciné films were digitized, and the coordinate data entered into a microcomputer to calculate joint moments and muscle, tendon and bone stresses from the force platform recordings. The reproducibility of joint location ranged from ±0·35 mm (S.D.) at the ankle to ±0·94 mm at the knee for the X-ray films, and ±0·42 mm at the ankle to ±0·74 mm at the ischium for the light films. Comparable accuracy was achieved for the light films because the orientation of the tibia could be determined directly from the position of the fibula, which was visible under the skin after the animals had been shaved. Based on the tibia's orientation and measured lengths of the animal's tibia, femur and distance from the ischium to the hip, the knee and hip coordinates could be calculated using plane geometry.

In vivo *tendon force measurements*

As part of a related study (Biewener *et al.* 1988), we made *in vivo* recordings of the forces exerted by the gastrocnemius and plantaris muscles from a tendon buckle force transducer (Loeb *et al.* 1985; Walmsley *et al.* 1978) implanted on the tendons of these muscles. This was done to test the reliability of our force platform/ciné analysis for calculating muscle forces in these muscles. The transducer recorded the summed force of the gastrocnemius and plantaris muscles. Because the fibre cross-sectional area of the soleus is less than 2 % of that of the other two muscles, its contribution could be ignored. No significant decrease in weight support was observed in the experimental *versus* control hindlimb force recordings and essentially equivalent results were obtained from the direct and indirect measures of muscle force. Consequently, we report here only the muscle and tendon stresses calculated from the direct recordings of muscle force.

Calculation of bone stress

Calculations of bone stress in the femur and tibia were based on a linked-segment free-body analysis of these two elements, following the approach used previously for chipmunks and ground squirrels (Biewener, 1983) and horses (Biewener *et al.* 1983*a*). As we have shown (Biewener *et al.* 1983*a*), this approach is sensitive to potentially large errors in stresses calculated to act at the bone's midshaft (compared with *in vivo* bone strain data from rosette strain gauges), resulting from relatively small errors in determining the net bending force acting on the bone. However, as direct recordings of bone strain are not feasible for most animals smaller than 0·5 kg body mass, the force platform/kinematic approach must be relied on to estimate skeletal stresses in small animals. In doing so, the specific stress values computed for each bone should be treated with some caution, and greater emphasis placed on relative comparisons among different locomotor activities. The greater number of muscles acting across the femur (at the hip and knee) further limits the reliability of the peak stresses computed for this bone. The extremely good correlation we achieved between direct and indirect measurements of muscle force at the ankle, however, indicates that our force analysis of the tibia was fairly accurate.

In situ *and anatomical measurements*

After all experimental recordings had been completed, the animals were anaesthetized with sodium pentobarbitol to calibrate the tendon force transducer *in situ* and measure maximal isometric force of the gastrocnemius and plantaris muscles. The animals were then killed and the relevant bones, muscles and tendons of the hindlimb dissected free to measure their masses, moment arms and

Table 1. *Anatomical data (values are the mean ±s.d. for nine kangaroo rats: body mass, 103 ± 15 g)*

	Tibia	Femur	
Bone			
Length (mm)	47·0 ± 2·1	31·0 ± 3·2	
Diameter (mm)	2·66 ± 0·23	2·62 ± 0·19	
Area (mm^2)	3·10 ± 0·54	2·80 ± 0·33	
Second moment of area (mm^4)	2·26 ± 0·59	2·25 ± 0·67	
Muscle	Gastrocnemius	Plantaris	Soleus
Mass (g)	1·13 ± 0·22	0·30 ± 0·06	0·05 ± 0·002
Fibre length (mm)	9·60 ± 1·23	7·16 ± 1·48	10·42 ± 1·57
Fibre angle	20 ± 3	22 ± 4	12 ± 2
Fibre area (mm^2)	113 ± 26	41 ± 10	5 ± 3
Moment arm (mm)	5·6 ± 0·4	5·6 ± 0·4	5·6 ± 0·4
Tendon			
Effective length (mm)*	37·6 ± 2·5	66·1 ± 3·2	36·2 ± 2·4
Mean area (mm^2)	1·04 ± 0·17	0·57 ± 0·18	

* Calculated as length from tendon origin to insertion minus muscle fibre length (after Alexander & Vernon, 1975).

geometric dimensions. The cross-sectional geometry of the femur and tibia was determined at the midshaft by photographing the sectioned bones, then magnifying (35×) and digitizing the cross-sections to calculate cortical area and second moment of area. Muscle fibre cross-sectional areas were calculated from muscle mass, fibre length and pinnation angle according to the method of Calow & Alexander (1973). The anatomical data for the bones, muscles and tendons are given in Table 1.

Results

Acceleration during hopping versus *jumping*

During steady-speed hopping, forces exerted on each hindlimb rose from 1·0 times body weight at a speed of 0·7 m s^{-1} to 4·0 times body weight at a speed of 3·1 m s^{-1}. During jumping, peak forces acting on each limb were much greater than during hopping, reaching 9·6 times body weight at the highest jumps recorded. These 50 cm jumps correspond to a height roughly equal to 10 times the resting hip height of the animal.

Bone stresses

Peak stress in the femur and tibia increased linearly with increased speed during steady-speed hopping. Fig. 1A shows the increase in peak compressive (negative) stress acting in the caudal midshaft cortices of these two bones *versus* hopping speed. Both bones were subjected primarily to bending (Fig. 2), with net tensile stresses acting in their cranial midshaft cortices. Bending of the tibia was due to off-axis loading of the bone by the ground reaction force, whereas bending of the femur resulted from its curvature (concave caudal), offsetting the off-axis (cranial) loading by the ground reaction force of this bone. Although not shown, peak tensile stresses increased in a similar fashion, indicating that a uniform distribution of stress was maintained throughout the observed range in hopping speed. At the fastest hopping speed recorded (3·1 m s^{-1}), peak stresses were −34 MPa (caudal) in the femur (cranial: +6 MPa) and −31 MPa (caudal) in the tibia (cranial: +22 MPa). The regression slopes for each bone were essentially the same and match the increase in peak stress in the ankle extensor muscles *versus* speed (Biewener *et al.* 1988).

During jumping, peak stresses as high as −145 MPa (caudal) acted in the tibia (cranial: +131 MPa) and −132 MPa (caudal) in the femur (cranial: +101 MPa) in the highest jumps (50 cm) observed. Peak stresses for jumps greater than or equal to 40 cm in height averaged −110 ± 25 MPa (+98 ± 23 MPa in tension) in the tibia

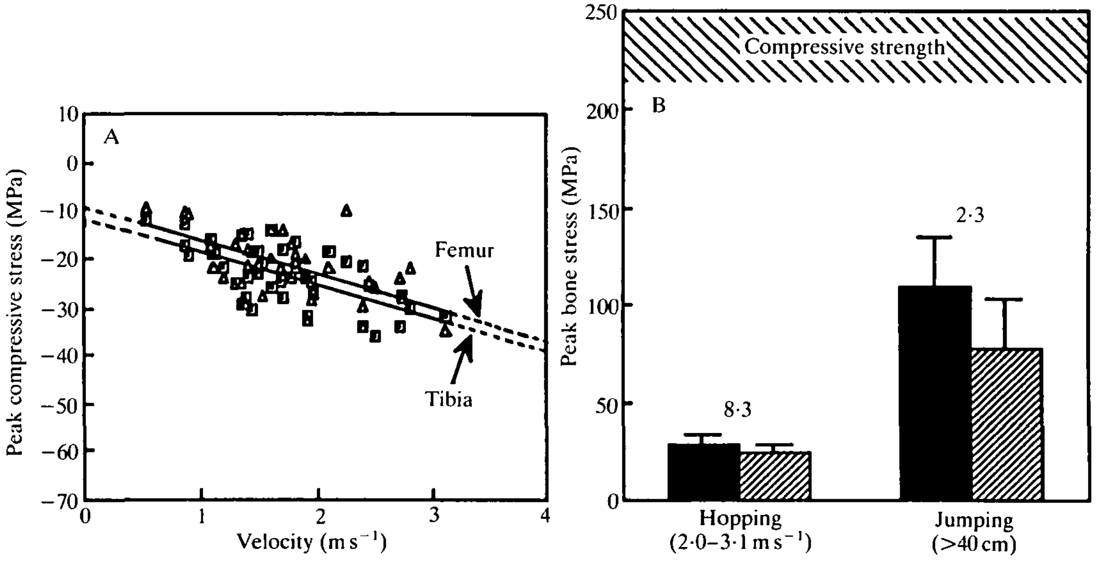

Fig. 1. (A) Peak compressive stresses acting at the midshaft (caudal) cortices of the tibia (squares) and femur (triangles) plotted *versus* steady hopping speed. The least squares regression for the tibia (solid line, slope = −6·75) and femur (dashed line, slope = −6·86) are shown. The regression slopes for these two bones were not significantly different. (B) A histogram of the peak (compressive) stresses in the tibia (filled columns) and femur (cross-hatched columns) during steady-speed hopping (averaged over 2·0–3·1 m s^{-1} range of speed) *versus* jumping (≥40 cm). The hatched area above depicts the range of compressive strength values reported for mammalian cortical bone (mean 230 MPa). These stress levels indicate a safety factor to failure in these two bones of 8·3 during steady hopping ($N = 15$) and 2·3 during jumping ($N = 11$). Error bars represent the s.d. about the mean.

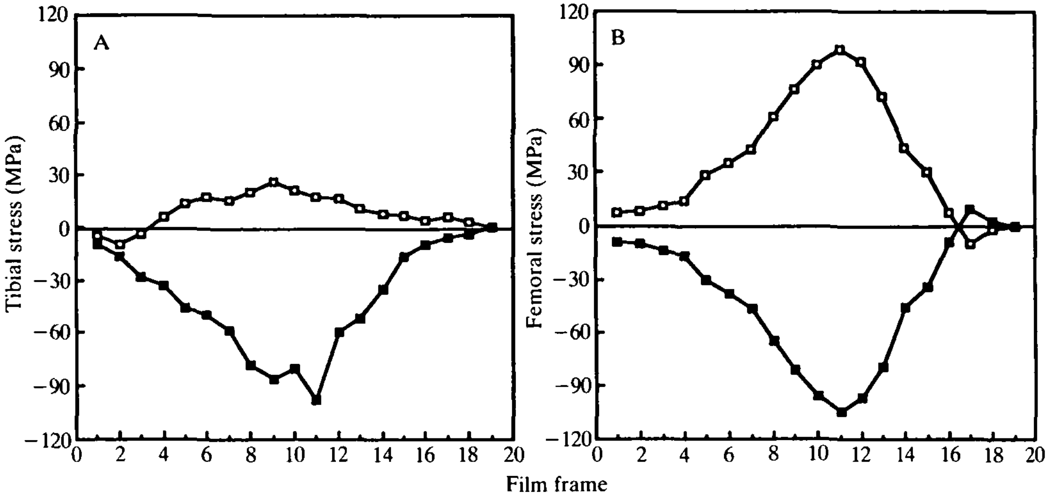

Fig. 2. Representative stresses acting in the cranial and caudal midshaft cortices of the tibia and femur during a vertical jump of 40 cm. Bending predominates in each bone placing the caudal cortex in compression (■) and the cranial cortex in tension (□). In the tibia (A), which is straight at its midshaft, bending was due mainly to off-axis loading by the ground reaction force in the caudal direction. In the femur (B), off-axis loading in the cranial direction by the ground reaction force was exceeded by bending induced by the bone's curvature in the caudal direction.

and −78 ± 26 MPa (+62 ± 29 MPa in tension) in the femur. These stresses were generally three times greater than those acting at the highest hopping speeds observed (Fig. 1B). Reported values for the compressive strength of bone average about 230 MPa (Wainwright *et al.* 1976; Currey, 1984), so the safety factor of these two bones decreases from about 8·3 during hopping to 2·3 during jumping. Reported values for the tensile strength of bone average about 150 MPa (Currey, 1984). Hence, as the values of peak tensile stress were generally 15–20 % lower than the values of peak compressive stress in these two bones, the safety factor of these bones for tensile failure was slightly lower (1·9 during jumping) than that for compressive failure.

Muscle and tendon stresses

Much greater stresses were also developed in the gastrocnemius and plantaris muscles and their tendons during jumping than during steady-speed hopping (Fig. 3). Stresses in these two ankle extensors increased from 33–110 kPa during steady-speed hopping (0·6–2·1 m s^{-1}) to as high as 350 kPa for the highest jumps recorded. Given that the maximum isometric force exerted by these muscles *in situ* is 200 kPa (Biewener *et al.* 1988), the muscles must have been actively stretched and fully recruited to exert these very high (1·75 times maximum isometric) levels of force. These jumps characteristically followed landing from a previous jump, providing the means for active stretching of the ankle extensors. Even so, these

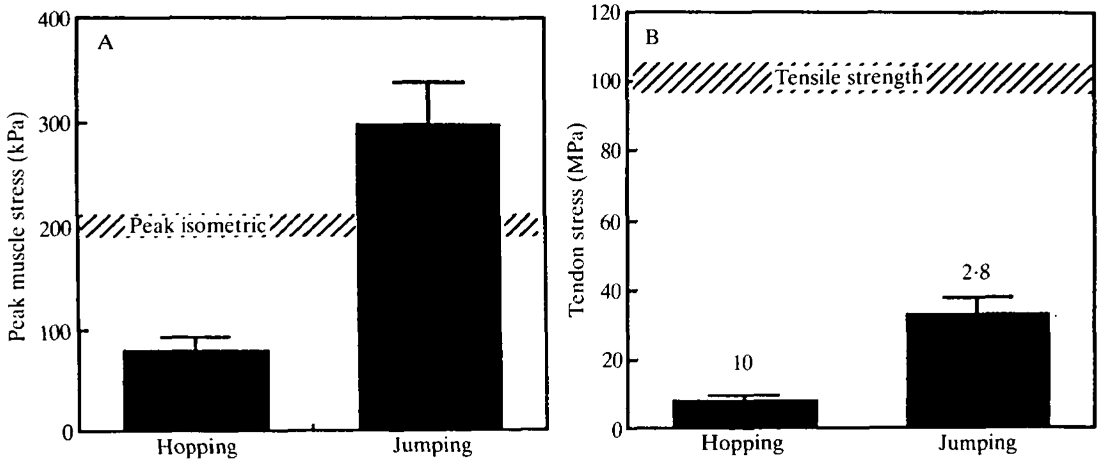

Fig. 3. (A) A histogram of the peak stresses acting in the ankle extensor muscles during steady-speed hopping (1·6–2·0 m s^{-1}, $N = 8$) *versus* jumping (⩾40 cm, $N = 7$). The hatched bar depicts the range of peak isometric stress values (mean 200 kPa) measured *in situ* on the same muscles. For these high jumps, the muscles must have been actively stretched and fully recruited to achieve stresses 1·75 times maximum isometric stress. Data from Biewener *et al.* (1988). (B) A histogram of the peak stresses acting in the tendons of the gastrocnemius and plantaris muscles during steady-speed hopping *versus* jumping. The hatched bar depicts the range of tensile strength values reported for mammalian tendon (mean 100 MPa; Bennett *et al.* 1986). These stress levels correspond to a safety factor to failure of 10 during steady-speed hopping and 2·8 during jumping. Error bars are the S.D. about the mean.

levels of force were remarkably high, and may reflect an underestimate of peak isometric tension resulting from our failure to stimulate the whole muscle. We were careful to minimize the likelihood of this, using supramaximal stimulation *via* the nerve to measure peak isometric force at the optimal length (for details, see Biewener *et al.* 1988). Significantly higher stresses have been reported for muscles in the rat (270–320 kPa; Wells, 1965). However, other studies of rodent muscles, including those of the rat (see Close, 1972; Prosser, 1973), report peak isometric stresses that more closely match our value for these kangaroo rat muscles (range: 180–200 kPa). Similar peak isometric stresses have been reported for frog sartorius (200 kPa; Hill, 1970) and cat soleus and gastrocnemius (190–240 kPa; unpublished data from our laboratory).

Stresses in the tendons of these two muscles (calculated as an average stress for the two tendons as a functional unit) increased from 5–10 MPa during steady-speed hopping to 36 MPa for jumps of 50 cm height, averaging 32 MPa for jumps ⩾40 cm (Fig. 3B). The low stress levels during hopping underlie the limited capacity of these tendons to store elastic strain energy. Given that the tensile strength of vertebrate tendon is about 100 MPa (Bennett *et al.* 1986), the safety factor of these tendons varies from 10 during hopping to 2·8 during jumping, consistent with the change in safety factor observed for the tibia and femur.

Discussion

At all levels of locomotor activity that we examined, peak stresses acting in the three structural components of the kangaroo rat's hindlimb skeleton (muscle, tendon and bone) are closely matched to the strength of each support element, reflecting integrated design of the hindlimb as a whole. The maximum forces exerted on the ground when kangaroo rats jump to heights as great as 50 cm are three times greater than those exerted when they hop at their fastest steady speed. These values correspond to ground reaction forces equal to 9–10 times the animal's own weight (exerted on each hindlimb separately) and jump heights equal to 10 times the animal's hip height. In association with these large forces, the stresses produced in the ankle extensor muscles, tendons and bones of the hindlimb during maximal recorded jumps are 3–4 times greater than those observed during steady-speed hopping. Safety factors for these elements decrease to nearly 2, approaching the limit observed for most biological structures that have been studied (Alexander, 1981; Biewener, 1983; Biewener *et al.* 1983*b*; Lowell, 1985).

If the ankle extensor tendons of this species were more slender, their ability to save energy by elastic storage and recovery would be greatly improved (generally, a 50 % reduction in tendon cross-sectional area will result in roughly a four-fold increase in total strain energy stored for tendons of equivalent length). However, the forces produced to achieve the accelerations we recorded when the animals jumped would place thinner tendons at great risk of being ruptured. When viewed in the context of maximal acceleration, rather than useful energy savings, the hindlimb of the kangaroo rat is not 'overbuilt'. Indeed, the safety factors for the bones, muscles and tendons of this species are similar to those measured in other mammalian species during strenuous activity (Alexander, 1974; Alexander *et al.* 1981; Alexander & Vernon, 1975; Biewener, 1983; Biewener *et al.* 1983*b*; Biewener & Taylor, 1986; Rubin & Lanyon, 1982).

In a related study (Perry *et al.* 1988) we compared stresses developed in the ankle extensors of kangaroo rats and white rats at their 'preferred' locomotor speeds. We found that similar stresses (70 kPa) acted in the muscles of both species at their preferred speeds ($1{\cdot}5\,\mathrm{m\,s^{-1}}$), suggesting an equal capacity to increase muscular force (for more demanding activities) about three- to four-fold for each species. Yet, if the kangaroo rat is designed for acceleration as we propose, why should it exhibit similar muscle stress under comparable performance to a less cursorial animal? Although the capacity for an increase in muscle force is *proportionately* the same in these two species, it is misleading in that the *absolute* increase in force production by the hindlimb muscles of the kangaroo rat greatly exceeds that of the white rat. Though *D. spectabilis* is half the size of the white rat, the muscles of the kangaroo rat exert 25 % greater force than the same muscles of the white rat at their preferred speeds. Normalized for differences in body weight, the kangaroo rat muscles exert three times greater force than that exerted by the white rat muscles. Similar stresses act because the fibre cross-sectional area of kangaroo rat muscles are proportionately larger. Therefore, the capacity of the kangaroo rat to increase absolute muscle force and, hence, peak acceleration is 3–4 times greater than that of the white rat. A major component of this increased force requirement clearly depends on the use of its hindlimbs for locomotor support compared with the quadrupedal locomotion of the white rat.

Acceleration to avoid predation

Behavioural observations of predator avoidance (owls and rattlesnakes), coupled with studies of the morphology and auditory sensitivity of the greatly expanded middle ear cavity of the kangaroo rat (Webster, 1962; Webster & Webster, 1980), provide direct evidence that the jumping ability of these heteromyid rodents is the means by which the animals avoid predation. Webster found that the large volume of the middle ear cavity (auditory bulla) in the kangaroo rat skull diminishes damping of the tympanic membrane, dramatically increasing the animal's sensitivity to low-frequency (2000 Hz) sounds. Both nocturnal predators were found to produce sounds at this low frequency when approaching the animal, warning the kangaroo rat to jump vertically to avoid being caught (analogous to the conditions of our experiment). Hence, the competing selective demand for rapid vertical acceleration has resulted in tendons too thick for useful elastic energy storage during steady-speed hopping.

It should be noted that this interpretation depends on the view that the top *steady-state* hopping speeds of this species in their natural habitat are not much greater than those recorded in this study ($3{\cdot}1\,\mathrm{m\,s^{-1}}$). Presumably, if these animals hop at much greater steady-state speeds in the field, stress levels in their tendons (muscles and bones) would be increased, possibly enabling storage of significant elastic strain energy. Kenagy (1973) has reported top speeds of a smaller heteromyid (*D. merriami*, 35 g) hopping at nearly $9\,\mathrm{m\,s^{-1}}$ in the field. However, neither the method of estimating the animals' speeds nor the distance over which speed was measured were given. We believe that by taking advantage of their hindlimb accelerative ability, these species may be capable of achieving such high speeds for short sprints. However, it seems unlikely that such high speeds could be maintained over a sufficiently large distance for elastic energy savings to be significant.

Safety factor of tendon versus *muscle*

An important problem in the design of any structural support element is how large the safety factor needs to be. Alexander (1981, 1984) has attempted to address this problem for biological support structures by modelling the theoretical loading distribution of a structure throughout a lifetime of use relative to the variation in its strength. As variation in strength or, more importantly, variation in peak loads that a structure must bear during its use decreases, selection may be expected to decrease the safety factor of the structure. Alexander noted that the cost of building and maintaining the structure, the cost of bearing the structure's weight, and the cost of the structure's failure to the organism represent additional factors that probably affect the safety factor of a given structure. Unfortunately,

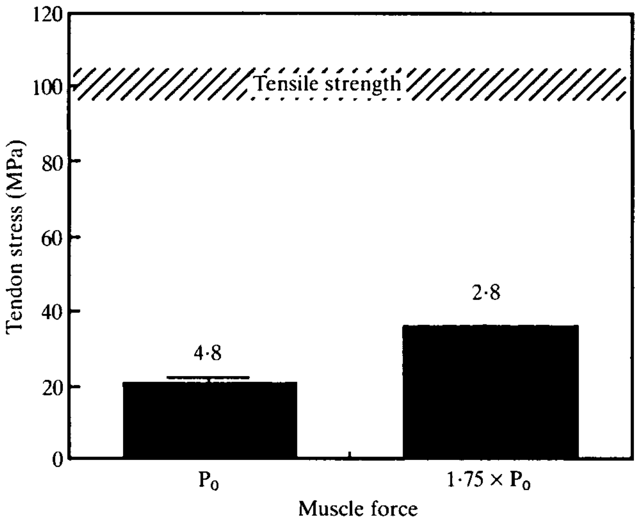

Fig. 4. A histogram of tendon stress developed when the muscles exert their maximum isometric force measured *in situ versus* when the muscles exert 1·75× maximum isometric force ($P_0 = 350$ kPa muscle stress). These very large stresses were developed when the animals jumped to the highest recorded height of 50 cm. The comparatively low safety factor (2·8) of these tendons reflects the well-defined maximum force they must bear during use (limited by the force-generating ability, or fibre cross-sectional area, of the muscles).

only few data are available for real biological variation in the strengths of structures (Alexander *et al.* 1984), fewer data for the variation in loading that biological structures experience in their natural habitat over a lifetime of use, and none for building or maintenance costs. Indeed, it is extremely difficult to record or to estimate accurately the frequency distribution of forces most structures must bear over a lifetime of use. Lowell (1985) has successfully accomplished this for limpets, whose shells are subjected almost solely to the prying forces of starfish, showing that increased variance in shell strength was correlated with an increase in safety factor.

Another biological structure that possesses a fairly well-defined loading history is the vertebrate tendon (and arthropod apodeme). Because the forces that a tendon must bear are limited by the force-generating capacity of the muscle to which it is attached, the area of tendon needed to resist these forces is closely defined by the fibre cross-sectional area of the muscle (as the force-generating capability of the myofilaments is uniform for vertebrate striated muscle; Close, 1972; Hill, 1970; Prosser, 1973; Wells, 1965). Theoretically, then, as long as a tendon has a safety factor greater than one, the muscle will always rupture before the tendon fails, given failure arising from a single (accidental) loading event. If we compare the stresses acting in the plantaris and gastrocnemius tendons of the kangaroo rat, in relation to the isometric force exerted by these two muscles, we find that the tendons have a safety factor of 4·8 (Fig. 4). When we consider the forces exerted by these two muscles during maximal jumps (50 cm), the tendon's safety factor is lowered to 2·8. Although substantially higher than one, a 'low' safety factor such as this (most estimates of biological safety factors fall in the range 3–5; Alexander, 1981) is consistent with the limited range (low variance) of peak force that the tendon must withstand.

In conclusion, the design of biological structures built of similar materials is probably dictated by the need to maintain roughly equivalent safety factors over the range of forces they must bear. Other factors, such as variation in peak load, cost of failure or costs of maintainence and use of the structure, may lead to smaller changes in the overall magnitude of safety factor for a structure. In the case of vertebrate tendon, elastic energy storage capability is one key factor that will favour reduction in safety factor. This appears to be an important energy-saving mechanism in the limb design of several large mammals. However, we have shown here for the kangaroo rat that other locomotor capabilities, such as rapid acceleration, may compete with elastic energy saving, dictating increased tendon area (lower strain) to withstand increased force generation by the muscles. The disproportionate increases in size of all three skeletal elements of the kangaroo rat hindlimb (muscles, tendons and bones) are well matched to one another. Whereas large animals may move more frequently at steady speeds (conditions best suited for elastic energy storage and recovery), small animals appear to place greater reliance on their ability to accelerate (or decelerate) rapidly, in which elastic energy saving is not important.

This work was supported by NSF grant PCMB 85-14899 to AAB. The authors are grateful to Mr Andrew Perry, Dr Norman Heglund and Dr Richard Taylor for their help in the experiments and comments on earlier drafts of the manuscript.

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