

THE UNIVERSITY OF CALGARY

The Relationship Between Body Mass and the
Capacity for Storage of Elastic Strain Energy
in Mammalian Limb Tendons

by

Colleen M. Pollock

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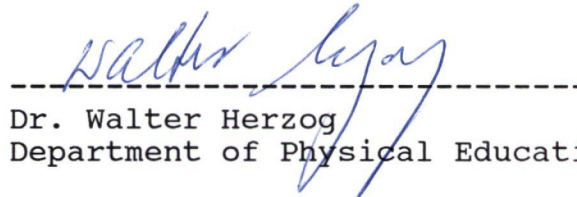
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "**The Relationship Between Body Mass and the Capacity for Storage of Elastic Strain Energy in Mammalian Limb Tendons**", submitted by Colleen M. Pollock in partial fulfillment of the requirements for the degree of Master of Science.



Dr. Anthony P. Russell
Supervisor
Department of Biological Sciences



Dr. Richard L. Walker
Department of Biological Sciences



Dr. Walter Herzog
Department of Physical Education



External Examiner
Dr. Nigel G. Shrive
Department of Civil Engineering

May 06 1991

Date

ABSTRACT

The purpose of this study was to determine the allometric relationship between the capacity for storage of elastic strain energy in the distal limb tendons and body mass, and the size dependent mechanism(s) (material and/or structural properties) that determine this relationship. The amount of strain energy stored and released by a tendon depends upon its material properties (elastic modulus and hysteresis) and the extension that occurs when it is loaded by an external force or its muscle. Thus the tendon material properties and cross-sectional area, as well as muscle dimensions (muscle force) in relation to body mass were analyzed in terms of their potential contribution to the elastic energy storage capabilities of tendon.

The material properties (i.e., elastic modulus and hysteresis) of the digital flexor, ankle extensor and digital extensor tendons from 23 quadrupedal mammals, ranging in body mass from 0.5 to 545 kg were determined via tensile tests. These functionally different tendons showed no significant differences in their material properties over the entire size range. Not only are they materially similar to one another, their material properties scale independent of body mass.

Morphometric analysis of the digital flexor, ankle extensor and digital extensor muscle-tendon units from 35

quadrupedal mammals ranging in body mass from 0.05 to 545 kg was carried out. The capacity for storage of elastic strain energy was found to scale with positive allometry, i.e., the scaling exponent is greater than one, for the spring-like tendons (digital flexors and ankle extensors), but scaled isometrically for the digital extensor tendons, indicating that the spring-like tendons of large mammals potentially can store more elastic strain energy than can these same tendons of smaller mammals. Muscle fibre cross-sectional area scales with positive allometry (and consequently muscle force), and tendon cross-sectional area scales isometrically. Thus the amount of stress a tendon can be expected to experience, as indicated by the muscle/tendon area ratio, scales with positive allometry, (i.e., tendon stress increases with body mass). Thus the greater capacity for storage of elastic strain energy in large mammals is due primarily to their relatively stonger muscles, which can impose higher stresses and consequently strains on their tendons than can the same muscles of smaller mammals.

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List of Abbreviations and Symbols

a	proportionality coefficient, or elevation of allometric equation.
a_c	common proportionality coefficient.
a_j	area of muscle fibres of j^{th} member of a muscle composed of more than one head.
A_m	total cross-sectional area of the fibres of a muscle.
A_t	cross-sectional area of tendon.
b	regression coefficient, allometric exponent or slope of allometric equation.
b_c	common regression coefficient.
CDE	common digital extensors.
DDF	deep digital flexors.
E	modulus of elasticity for tendon.
f	tendon tensile force.
F_g	ground reaction force.
F_m	muscle force.
GAS	gastrocnemius.
GPa	Gigapascals
H	hysteresis
l	extension of material when loaded (see figure 2.2).
L	muscle-tendon length factor.
l_j	length of muscle fibres of j^{th} member of a muscle composed of more than one head.
L_m	length of muscle fibre.
l_s	length of a selected portion of tendon for tensile tests.
L_t	effective length of tendon.

ΔL_t tendon extension at max. stress.
 M_b body mass.
MPa Megapascals.
 m_j muscle mass of j^{th} member of a muscle composed of more than one head.
 M_m mass of a muscle.
 m_s mass of a selected portion of tendon.
P probability
PLA plantaris.
r moment arm about the ankle joint (distance between ankle joint and muscle force vector).
R moment arm of the ground reaction force (distance between ground reaction force vector and ankle joint).
U tendon max. capacity for elastic strain energy.
X independent variable in allometric equation.
Y dependent variable in allometric equation.
 Σ sum of.
 ϵ in vitro tendon strain.
 ϵ_t max. in vivo tendon strain
 θ angle of pinnation.
 σ in vitro tendon stress.
 σ_m max. in vivo muscle stress (0.3MPa).
 σ_t max. in vivo tendon stress.
 ρ_m density of muscle.
 ρ_t density of tendon.
 α scales to or is proportional to.

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CHAPTER 1

GENERAL INTRODUCTION

Tendons situated in the distal limb of mammals are generally thought to function as stiff biological springs, alternately being stretched and recoiling with each stride (Alexander, 1984). When a tendon is stretched, work is done on it, and elastic strain energy stored in it. This is a form of potential energy (the capacity to do work) (Alexander, 1983). The amount of strain energy stored depends upon the amount of extension, which is largely determined by the elastic properties of the tendon and the amount of force exerted upon it. Composed primarily of collagen, which provides their mechanical properties, tendons of the distal limb generally have both high tensile strength and elastic modulus (stiffness), can be stretched reversibly up to 6% of their resting length, and are very resilient, allowing them to absorb and release energy (Butler et al., 1978; Ker, 1981; Woo, 1982; Bennett et al., 1986; Shadwick, 1990). These properties potentially allow for large amounts of elastic strain energy to be stored in tendons which experience high stresses, such as those incurred during the support phase in fast locomotion (Alexander, 1984). At each step (during the support phase), animals with erect limb posture (mammals and birds) lose and then regain kinetic and gravitational potential energy.

Part of this energy is degraded as heat by the muscles being stretched and is later replaced by muscles contracting. Most is stored, however, as elastic strain energy in the tendons and then released in elastic recoil, requiring no expenditure of metabolic (muscular) energy (Alexander, 1980, 1983 & 1984; Alexander and Vernon, 1975; Cavagna et al., 1977).

A systematic decrease in the net cost of transport (the metabolic energy required in excess of resting rates for a unit mass to travel a unit distance) for mammals and birds as body mass increases has been well documented (Tucker, 1970; Taylor et al., 1970; Taylor, 1977; Taylor et al., 1982; Strang and Steudel, 1990). This means that larger species are capable of moving each kilogram of their body mass through a distance of 1 meter at a lower metabolic cost than the smaller ones. One possible mechanism that may explain this pattern is a size-dependent variation in the extent to which elastic strain energy in tendons of the distal segments of the limb can be used to reduce the amount of energy input required from muscle contraction to maintain steady state locomotion (Biewener et al., 1981; Strang and Steudel, 1990). For validation of this proposed energy saving mechanism, however, there is a need to show that storage of elastic strain energy in these tendons does indeed scale with body size at a rate greater than one. In other words, that limb tendons of larger mammals (and/or birds) have a higher capacity for storage and subsequent

release of elastic strain energy than do those of smaller mammals.

The primary objectives of this study were to investigate the allometric relationship between body mass and the capacity of the distal hind limb tendons to store elastic strain energy, and to determine the size-dependent mechanical and/or structural properties that cause this relationship in mammals. The first part of this study investigates the possibility of a size-dependent relationship between the tendon material properties and body mass. The premise for this is that the distal limb tendons of larger mammals have different material properties that endow them with a greater capacity to store elastic strain energy compared to the same (homologous) tendons of small mammals. The second part of this study consists of a morphometric analysis of the muscles and tendons of the distal segments of the hind limb. The premise for this is that there is a difference in the structural design of the muscle and/or tendon unit in larger mammals that allows for greater amounts of elastic strain energy to be stored in the tendons than is possible in the homologous tendons of smaller mammals. If it can be shown that the capacity for storage and release of elastic strain energy increases at a rate greater than body mass increase, then it can be surmised that this mechanism is, at least in part, responsible for the lower transportation costs of large mammals.

CHAPTER 2

BACKGROUND

2.1 Storage of Elastic Strain Energy

With each stride, a running mammal loses and then subsequently regains kinetic and gravitational potential energy as a result of its changing relationships with the ground and the mechanical properties of its limbs. As the foot lands on the ground the body is decelerated forward and downward (Heglund, 1980), the ground reaction forces increase, the angles of the lower limb joints (ankle, wrist, metatarso- or metacarpo-phalangeal) increase, lengthening the muscles and tendons on the caudal side of these joints (Alexander, 1974; Alexander and Vernon, 1975; Biewener et al., 1981; Goslow et al., 1981; Alexander, et al., 1982). In other words, these muscle-tendon units are stretched by the impact forces. During this phase of the stride, both kinetic and gravitational potential energy decrease (Alexander and Vernon, 1975; Cavagna et al., 1977). Some of the kinetic and gravitational potential energy is lost as heat by the muscles stretching, being compelled to do negative work. As well, some of this energy is briefly stored as elastic strain energy in the muscles and tendons that are stretched by the impact forces (Alexander, 1980, 1983 & 1984; Cavagna et al., 1977). In the latter half of

contact with the ground, as the limb pushes off, the body must be accelerated forward and upward (Heglund, 1980), the forces on the muscles and tendons decrease, the muscles and tendons shorten and the angles of the joints decrease (Alexander, 1974; Alexander and Vernon, 1975; Biewener et al., 1981; Goslow et al., 1981; Alexander, et al., 1982). Both kinetic and gravitational potential energy increase during this latter half of contact with the ground (Alexander and Vernon, 1975; Cavagna et al., 1977).

Evidence in favor of the idea of elastic energy storage first came from a studies where the mechanical (kinetic and gravitational potential) energy changes that occur during fast locomotion were compared with O₂ consumption (metabolic energy consumption). It was shown that the metabolic machinery supplies a fraction of the power required to lift and reaccelerate the centre of mass (Dawson and Taylor, 1973; Cavagna et al., 1977). Thus the rest of the energy required to lift and reaccelerate the centre of mass had to be accounted for by some mechanism other than aerobic muscular metabolism. Elastic energy must be stored transiently in stretched tendons and muscles during hopping or running, similar to the way energy is stored in the spring of a pogo stick or bouncing ball (Alexander and Vernon, 1975; Cavagna et al., 1977; Alexander, 1984).

A muscle exerting isometric stress is capable of stretching elastically by 2 - 3% of its fibre length (Rack and Westbury, 1974; Alexander and Bennett, 1977). Since

these distal limb muscles generally have short fibres and long tendons this elastic extension of the muscle is so small compared to the extension of the tendons which exert the same force, that the elastic strain energy stored in the muscle fibres is trivial (Alexander and Bennett-Clark, 1977; Alexander, 1984). Most of the elastic extension is in the tendon, therefore it follows that this is where most of the elastic strain energy is stored, and any elastic energy storage in the muscle can be effectively ignored. Thus, as the animal runs the distal limb tendons operate as passive biological springs, alternately stretching and recoiling with each step, storing and releasing elastic strain energy (Alexander, 1980, 1983 & 1984).

Figure 2.1 illustrates how energetic savings are made by exchange between kinetic and gravitational energy (A) on one hand and elastic strain energy (B) on the other. The kinetic and gravitational energy lost in the first half of contact with the ground is replaced in two ways; 1) by muscles contracting, doing positive work and 2) by elastic recoil of the tendons. This elastic recoil converts most of the stored strain energy back into gravitational potential and kinetic energy before the foot leaves the ground. If there were no elastic elements the contractile elements of the muscles would have to do negative work ($-A$) followed by positive work (A) equivalent to the amount of kinetic and gravitational potential energy fluctuations in each step.

Because the tendons (elastic elements) store and release elastic strain energy, only negative work amounting to $-(A-B)$ and positive work amounting to $(A-B)$ have to be done. Both categories of work are reduced by a fraction B/A (Biewener et al., 1981).

It appears, however, that only large mammals benefit significantly from energy savings via storage and subsequent release of elastic strain energy (the dog, Alexander, 1974;

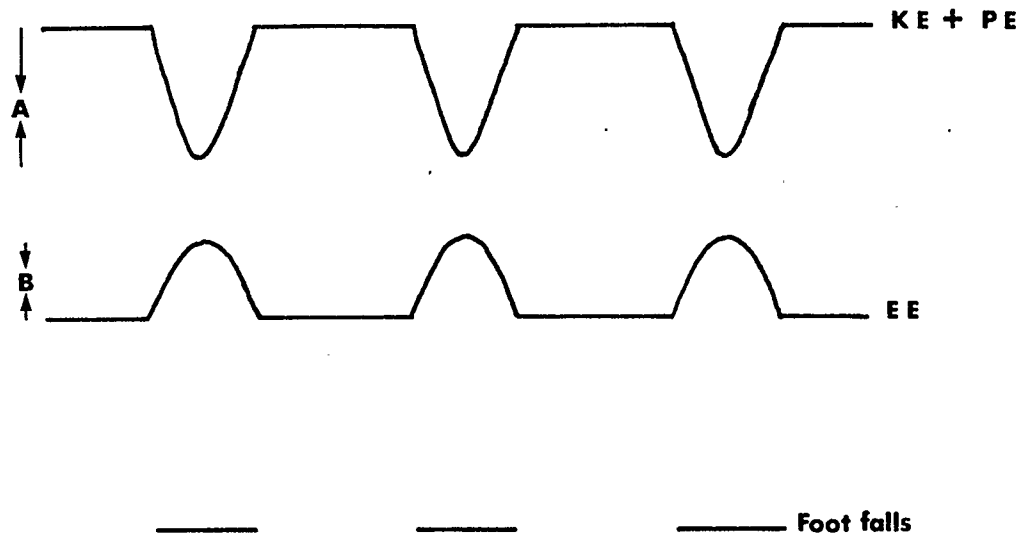


Figure 2.1. Elastic energy savings. The total kinetic energy (K.E.) and gravitational potential energy (P.E.) fall by an amount A in the first half of the step, and rise by A in the second half. The amount of elastic strain energy (E.E.) stored and released from the tendons is equivalent to an amount B . Thus, due to an exchange between these types of energy, the amount of negative and positive work the muscles have to do is reduced by a fraction, B/A . The points when the foot is on the ground are also shown (adapted from Biewener et al., 1981 and Alexander, 1983).

kangaroo and wallaby, Alexander and Vernon, 1975; donkey, Dimery and Alexander, 1985; camel, Alexander et al., 1982; and deer Dimery et al., 1986) Only one small species, the kangaroo rat, has been tested with respect to energy savings by way of elastic energy storage (Biewener et al., 1981; Biewener and Blickhan, 1988). Here it was found that relatively little energy savings was obtained from the return of stored strain energy. Biewener et al., (1981) proposed that the kangaroo rat is unable to store large amounts of strain energy because its disproportionately thicker tendons do not develop strains as large as those seen in the wallaby or kangaroo. No similar investigations have been made for other small mammals. This conclusion (only large mammals can benefit from elastic strain energy storage) was also reached by derivation from allometric equations based on anatomical measurements of the digital flexors and ankle extensors (Alexander 1977; Alexander et al., 1981; Peterson et al., 1984). However, such conclusions could be altered if there has been an incorrect assumption regarding the uniformity of tendon stiffness (elastic modulus). Clearly, the size dependency of storage and release of elastic strain energy needs more study (Heglund et al., 1982b; Strang and Steudel, 1990).

This discrepancy between the apparent capability of large versus small mammals to store elastic strain energy suggests that scaling is involved. However, before dealing with the principles of scaling, the structural and

biomechanical properties of tendon that allow for storage of elastic strain energy will be discussed.

2.2 Structural and Material Properties of Tendons

When an elastic material is stretched, work is done on it, and strain energy stored by it. Figure 2.2 illustrates a visco-elastic material stretched by a force (F), deformed by an amount represented by l . The triangular area under the rising line represents the work done stretching the material. The amount, $F l/2$, closely approximates the amount of strain energy stored. This is a form of potential energy (the capacity to do work). The area under the descending line gives the work recovered in elastic recoil when the imposing force is removed, and the area between the two lines represents the amount of energy lost, due to viscous processes (hysteresis). From figure 2.2, the amount of strain energy stored depends on the the amount of force applied to the material, and the stiffness of the material. The amount of energy recovered in elastic recoil depends on the mechanical hysteresis of the material (Wainwright et al., 1976; Alexander, 1983). However, the situation will be different if the same force is applied to two bodies of different size. For example, the slope of the force-extension curve also depends on the cross-sectional area of the material under tensile load. By increasing the cross-

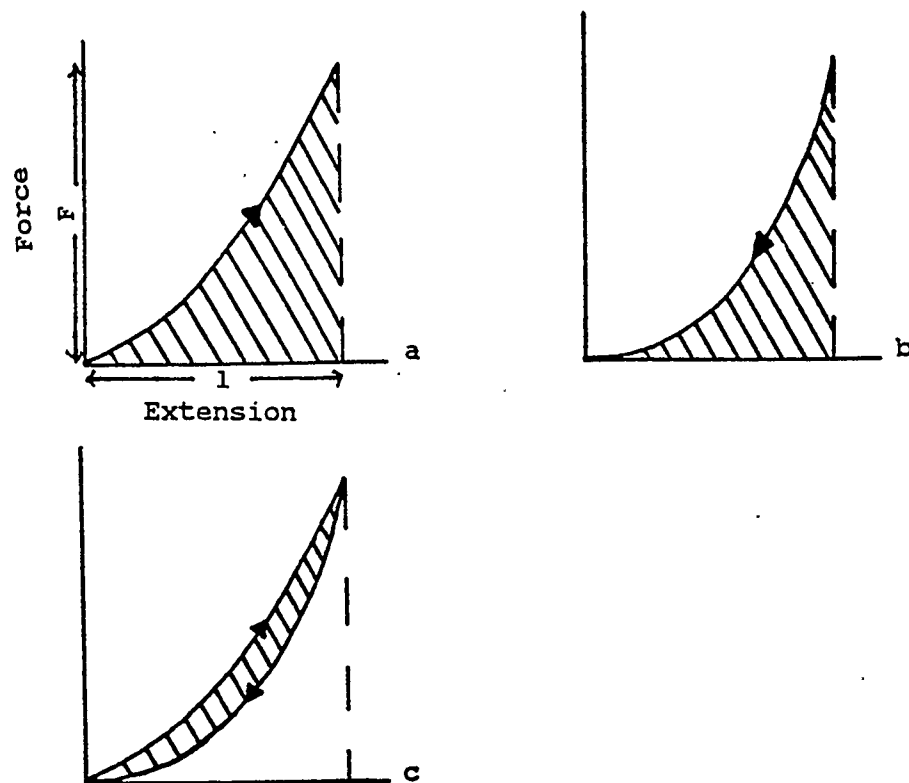


Figure 2.2. Schematic graphs of force against extension for a visco-elastic material that is stretched (a), then allowed to shorten (b) producing a hysteresis loop (c). (re-drawn from Alexander, 1983).

sectional area more material is available to carry the load, and it is thus able to withstand larger forces. However, for equivalent forces, the thinner material is stretched more and thus can store more elastic strain energy. To avoid problems due to changing dimensions, the force-extension curves are often adjusted (normalized) by dividing force by the material cross-sectional area, resulting in a tensile stress term, and by dividing extension by the initial unloaded length of the material, resulting in a strain term. The resulting stress-strain curve provides

mechanical (material) parameters that are independent of material dimensions (Butler et al., 1978).

The most common material parameters taken from the stress-strain curve are elastic modulus or stiffness (slope of the linear portion of the loading curve), mechanical hysteresis and amount of elastic strain energy stored and released per extension (Butler et al., 1978; Alexander, 1983).

By definition, tendons are the rope-like collagenous structures that connect muscle directly to skeletal elements. Tendons transmit tensile forces during muscle contraction. Thus, the muscle force applied to the proximal end of the tendon is a measure of the tensile force imposed on the tendon. The mechanical (material) properties of tendons are usually determined via tensile tests. When tendons are stretched in a tensile testing machine they produce similar force-extension curves to that shown in Figure 2.2. Composed of collagen (30% wet weight; 70-80% dry weight), which provides its mechanical properties, these visco-elastic structures generally have both high tensile strength (approx. 100 MPa) and elastic modulus (stiffness) (ranging from approx. 1.0 - 2.0 GPa), can be stretched reversibly up to 6% of their resting length, and are very resilient (i.e., they have a high capacity to absorb and release energy) (Butler et al., 1978; Ker, 1981; Woo, 1982; Bennett et al., 1986, Shadwick, 1990). This indicates that large amounts of elastic strain energy can be stored in

tendons that experience high stresses, such as occurs during the support phase in fast locomotion (Alexander, 1984).

From the above discussion it is evident that the quantity of strain energy stored and released by a tendon depends on its elastic modulus (stiffness), hysteresis (energy lost in viscous processes) and the extension that occurs when it is loaded by an external force or by the muscle to which it attaches. Thus, differences in tendon mechanical properties and cross-sectional area, as well as muscle dimensions (muscle force), may all contribute to differences in the elastic energy storage capability of tendon with increasing body size.

2.3 Principles of Scaling

Body size is one of the most important factors that affects the structure and function of organisms, and scaling deals with the structural and functional consequences of changes in body size among otherwise similar organisms (Schmidt-Nielsen, 1984). If two organisms are considered geometrically similar (isometric), any corresponding linear dimensions are in the same constant proportion ($L_1 \propto L_2$). As well, their areas and volumes will be in ratios related to their linear dimensions to the second and third power, respectively ($A \propto L^2$ $V \propto L^3$). Usually mass is an adequate measure of volume, for nearly all animals have densities

close to 1.0. Therefore the essentials of isometric geometry can be written as: $L \propto M^{0.33}$ and $A \propto M^{0.67}$ (Schmidt-Nielsen, 1984; Alexander, 1985).

Real organisms usually are not isometric, even when organized on similar patterns. In biology, such non-isometric scaling is often referred to as allometric scaling. An amazing number of morphological and physiological variables have been found to scale, relative to body mass, according to the allometric equation of the form:

$$Y = a X^b \quad (2.1)$$

where Y is the variable in question, and X is the body mass. The proportionality coefficient, a, is the intercept at unity (1 kg) and the scaling exponent, b, is the slope of the regression line (Schmidt-Nielsen 1984). Variations in the arithmetic rate of change of Y at different values of X, however, make arithmetic plots of body size relationships hard to draw and interpret. More commonly, for allometric relations the variables X and Y are transformed to logarithms, producing a straight line, and regression analysis applied to the data set. The aim of regression analysis is to find the straight line that, on average, describes the available data with the smallest errors (best fit). The line that is actually fitted is not $Y = a X^b$ but:

$$\log Y = \log a + b \log X \quad (2.2)$$

(Peters, 1983).

These allometric equations reflect generalizations, indicating how a variable is related to body size. The slope of the line (b) can take on different values and can be either positive or negative, depending on the variable being considered. If the variable Y , increases proportionately with body mass this reflects a simple proportionality and the slope of the regression line will be 1.0. If the variable in question increases out of proportion to the increase in body mass the regression line will then have a slope greater than 1.0. If the dependent variable increases at a slower rate than would be indicated by simple proportionality the regression line will have a slope less than 1.0. If we consider a quantity that does not change with body size, the slope will be zero. Finally, there are functions that decrease with increasing body size, and which yield regression lines with negative slopes (Schmidt-Nielsen 1984).

2.4 Rationale for Present Study

As mentioned above, previous comparative investigations of scaling of mechanical properties of tendons have been based on allometric equations derived from anatomical data (Alexander, 1977; Alexander et al., 1981; Peterson et al.,

1984). Scaling relationships of tendon mechanical properties have been derived assuming a constant (mass and species independent) elastic modulus, which has been critical to the formulation of ideas about elastic energy storage. Depending on whether tendon stress and strain have been considered to be independent of or dependent on body mass, the capacity to store elastic strain energy has been regarded as being either in proportion to body mass ($b=1$), or scaled somewhat higher ($b>1$). If the capacity to store elastic strain energy remains in proportion to body mass, this implies that there is no difference in the ability of small versus large mammals to store elastic strain energy. Conversely, if the capacity to store elastic strain energy scales somewhat higher ($b>1$), this implies that the tendons of large mammals have a greater capacity to store elastic strain energy than the homologous tendons of small mammals.

There are basically two parts to this study. The first deals with the material properties of tendons and their relationship with body mass. The second deals with the relationship between body mass and maximum capacity for storage of elastic strain energy in these same tendons.

The first question addressed in this study is: do the distal limb tendons of larger mammals have different material properties that result in a greater capacity to store elastic strain energy when compared to the same (homologous) tendons of small mammals? There have not been any studies in which direct measurements of elastic modulus

or hysteresis of mammalian tendons have been made with the purpose of comparing animals of different size. Stress, strain and elastic storage of strain energy have only been derived from allometric equations based on morphometric analysis of the digital flexors and ankle extensors. As well, elastic modulus has been assumed to be constant, independent of species and body size (Alexander, 1977; Alexander et al., 1981; Peterson et al., 1984).

Measurements of these properties from tendons over a large body size range must be made to determine whether elastic modulus or hysteresis scale with body mass.

There also appears to be some disagreement in the literature regarding the mechanical properties of tendons which do not experience loading during the support phase of the stride. One such muscle-tendon unit is the digital extensor, which is presumably active during the swing phase of the stride as opposed to the support phase (Ker et al., 1988; Shadwick, 1990) (however, electromyographic studies of this muscle-tendon unit during quadrupedal locomotion are needed to confirm this). Woo (1982) and Shadwick (1990), have shown that the digital flexors of mature pigs have a much higher elastic modulus (stiffer) than the digital extensors at equivalent strains. However, Ker et al., (1988) showed that there were no differences between the elastic modulus of the digital extensor of the cow and any of the other highly stressed tendons (including digital flexors) tested by Bennett et al., (1986). As there is a

considerable lack of consistency in the evidence regarding the stiffness of the digital extensors, the present study also includes investigations of the mechanical properties of these tendons from many quadrupeds over a large body size range.

As tendons are attached in series with their muscles, the tensile forces that they transmit, and the amount of strain they undergo is determined by the amount of force their muscles can exert. The maximum amount of force the muscles are capable of exerting will be determined via morphometric analysis of the muscle dimensions. Combined with information regarding tendon diameter, the maximum amount of stress the tendons could experience is also estimated. Finally by compiling information regarding tendon material properties and muscle-tendon dimensions over a large range of body sizes the scaling relationship of the capacity for storage of elastic strain energy is determined. This allows an answer to the question of whether the capacity for elastic storage of strain energy scales proportionally to body mass ($b=1$) (as predicted if tendon stress and strain are independent of body mass) or whether its importance increases with greater body mass ($b>1$).

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Specimens

Twenty seven species were examined in this study. These taxa were represented by 35 specimens, all of which were considered mature. Those species represented by more than one specimen are designated by a dagger (†). This selection of specimens covers the range of mammalian cursorial limb postures, from plantigrade through digitgrade to unguligrade species. The body mass range for each posture shows almost complete overlap with the others. At the lower end of the total body mass range are more generalized ambulatory mammals that show no specific cursorial modifications, (as defined by Jenkins, 1971 and Hildebrand, 1982) but may become behaviorally cursorial as a result of facultative changes in limb posture and cadence. With the exception of the domestic species, all animals were either zoo specimens or road kills. No laboratory specimens were used.

Cursors

-Plantigrade

† White-tailed jack-rabbit (Lepus townsendii) (2.2kg*, 3kg*)
 Grizzly bear (Ursus horribilis) (338kg*)

-Digitgrade

- † Domestic cat (Felis catus) (5.2kg, 6.9kg*)
- Snow leopard (Uncia uncia) (34kg*)
- † Domestic dog (Canis familiaris) (28kg, 36kg*)
- Lion (Panthera leo) (200kg*)

-Unguligrade

- Kirk's dik-dik (Madoqua kirkii) (3.9kg*)
- Indian hog deer (Cervus porcinus) (12.9kg)
- † Muntjac (Muntiacus muntjak) (11.1kg*, 11.4kg, 13.3kg)
- Pronghorn Antelope (Antilocapra americana) (20.4kg*)
- South African springbok (Antidorcas marsupialis) (28kg)
- Russian Saiga (Saiga tatarica) (28.5kg*)
- Mule deer (Odocoileus hemionus) (97.36kg*)
- † White tail deer (Odocoileus virginianus) (28.2kg, 76.64kg*, 97.68kg*)
- Scimitar-horned oryx (Oryx tao) (109.5kg)
- Eastern white-bearded gnu (Connochaetes taurinus) (204.5kg)
- † Elk (Cervus canadensis) (159.5*, 205kg*)
- Persian onager (Equus hemionus) (224kg)
- Cow (Bos taurus) (454kg*)
- Camel (Camelus dromedarius) (545kg*)

Ambulatory

- Gerbil (Meriones unguiculatus) (0.04kg)
- Wood rat (Neotoma sp.) (0.22kg)
- Guinea pig (Cavia porcellus) (0.35kg)
- Richardson's ground squirrel (Spermophilus richardsonii) (0.47kg*)
- Ferret (Mustela nigripes) (0.485kg*)
- Grey squirrel (Sciurus carolinensis) (0.55kg*)
- Muskrat (Ondatra zibethicus) (0.6kg)

*, asterisk indicates specimens which were employed in tensile tests.

The carcasses were obtained after the animals died or had been sacrificed for other purposes. All specimens and tissues were considered fresh at the time of collection, and were stored at -20°C until required for dissection or mechanical testing. Muscles and tendons from hind limbs only were used (with the exception of the Kirk's dik-dik, only one forelimb was made available for this specimen).

While only those specimens identified with an asterisk, in the above list, were subjected to the tensile testing, all (with the exception of the Kirk's dik-dik) were included in the limb morphometric analysis. Additionally, anatomical data for the following species were included in the limb morphometric analysis; these data were derived from literature sources.

Kangaroo rat (Dipodomys spectabilis) (0.08kg, 0.09kg, 0.10kg, 0.12kg) (Biewener et al., 1981)

Wallaby (Protemnodon rufogrisea) (10.2kg) (Alexander and Vernon, 1975)

Red Kangaroo (Macropus rufus) (40kg) (Alexander and Vernon, 1975)

Camel (Camelus dromedarius) (402kg) (Alexander et al., 1982)

The red kangaroo, wallaby and kangaroo rat are not considered to be strictly cursorial, but are rather designated as bipedal hoppers exhibiting ricochetel locomotion. Morphometric data from these specimens (bipedal hoppers) were included in Figures 4.4 through 4.11, but were not used in calculations for allometric constants.

3.2 Measuring Tensile Properties of Tendons

The mechanical properties of excised tendons are normally determined in vitro by tensile tests. The excised tissue is elongated at a prescribed rate while the changes in force and extension are simultaneously recorded. For this purpose a tensile testing machine (Monsanto Tensometer 10) was used. Tendons of the (1) digital flexor muscles

(plantaris, deep digital flexors [flexor hallucis and flexor digitorum longus]), (2) ankle extensor muscles (gastrocnemius and soleus [if present]), and (3) common digital extensor muscles were utilized. Measured segments of these tendons were clamped in various ways, the mode of clamping depending on tendon size. Two types of small aluminum clamps (2.5 x 3.5 cm) were used for the smallest tendons. One had either an emery paper or rubber gripping surface while the other had rounded serrated clamping surfaces. Larger stainless steel clamps (5 x 5 cm) with serrated gripping surfaces were used for the slightly larger tendons. For the largest tendons a cryo-jaw clamp was used, as described by Riemersa and Schamhardt (1982). This clamp resists slippage of tissue within the clamp for forces up to 13,800 N (sufficient force to break horse tendons). It also prevents tissue damage at the clamp site. Parallel marker lines were applied to the surface of the tendon. During testing the tendon was kept moist by dripping a 0.9% NaCl solution over the specimen. For the very thin tendons, however, the entire specimen was immersed in a chamber containing the saline solution in order to prevent drying out during testing.

The cross-head of the tensometer moved cyclically, alternately stretching the tendon and then allowing it to recoil, at a rate of 3-5 mm/min up to 5-6% strain, which is the range of strain to which most tendons can be extended reversibly without damage (Wainwright et al., 1976; Butler

et al., 1978). Ker (1981) and Shadwick (1990) have shown that at cycle frequencies ranging from 0.05 - 11 Hz, tendon material properties have virtually no frequency dependence, i.e., stiffness does not increase with strain rate. The load cell recorded the tensile force, while simultaneously the amount of tendon extension between the parallel marker lines was recorded using a video dimension analyzer (VDA) system. Measurements of length change were made in the central body of the tendon sample, well away from the clamps where slippage, tissue distortion and stress concentrations may occur (Ker 1981; Woo et al., 1980; Woo, 1982). From the video camera, information was sent through the VDA and viewed on a television monitor, in order to determine tensile extension of the tendon. As the distance between the two parallel marker lines increases during tensile loading, the output voltage of the VDA (extension signal) increased proportionally. However, at low strain levels, the strain computed by the VDA is sensitive to camera placement and orientation as well as the media through which the object is observed. At higher strain levels, the sensitivity of the system is reduced, and the strain computed by the VDA system approached the real strain (error decreases) (Lam et al., 1991). Such VDA errors were reduced in this study, by calibrating the voltage output of the VDA with each test, and by maximizing the image size on the television monitor screen.

Both the force and extension signals were sent to, and digitized at 10 - 50 Hz by either a 80386 PC or a MINC 11/23 lab computer, and stored on a disk. The extremely large data sets obtained from each test were reduced by removing every tenth, fifth or third point (depending on size of data set), producing manageable data sets for each cycle. These data were then used to calculate stress, strain, elastic modulus and hysteresis.

In all tests tensile stress was calculated as:

$$\sigma = f/A_t \quad (3.1)$$

force (in Newtons) divided by specimen cross-sectional area (in mm²), and expressed in Megapascals (1 MPa = 10⁶ N/m²).

Tendon cross-sectional areas were calculated as:

$$A_t = m_s/l_s \cdot \rho_t \quad (3.2)$$

by dividing the wet mass of a tendon sample by its length and density (approximated at 1.12 g/cm³; Ker, 1981; Shadwick, 1990). Strain was calculated as:

$$\epsilon = \Delta l_s/l_s \quad (3.3)$$

the change in length divided by initial length, as measured between the surface markers in tests with the video system.

A stress-strain curve is obtained when stress is

plotted on the Y axis against strain on the X axis. The slope of the linear portion of the loading curve is the ratio between the change in tensile stress and strain

$$E = \Delta\sigma/\Delta\epsilon \quad (3.4)$$

and is called the modulus of elasticity (Fig. 4.1). Elastic modulus is a measure of the elastic stiffness of the tendon. It is conventionally given the symbol E, and in this study is expressed in GigaPascals (GPa). The loading and unloading curves produce a loop because some of the work done stretching the tendons is lost viscously (degraded to heat) instead of being recovered in elastic recoil. Mechanical hysteresis (H) represents the mechanical energy lost (converted to heat) and may be calculated as the ratio of the area within the stress-strain loop (strain energy dissipated) to the area beneath the loading curve (total strain energy input), $(A/A+B)$ (Fig. 4.1). Resilience (R), the energy recovered due to release of elastic strain energy (elastic recoil), $(B/A+B)$, is the converse of hysteresis.

Allometric equations were obtained by least squares regression after transformation of the X and Y variables to logarithms. Body mass (X) was treated as the independent variable. The allometric equations are reported in the form $Y = a \cdot X^b$. Untransformed data were plotted on log-log scaled graphs (Schmidt-Nielsen, 1984; Peters, 1983). A Student's t test and the standard error of the slope were used to assign

95% confidence limits to the allometric exponent, b (Zar, 1984). The correlation coefficient (r) for each equation was also determined. Analysis of co-variance (Zar, 1984), was applied to the data to determine whether the slopes (allometric exponents, b) and the elevations (proportionality coefficients, a) of the allometric equations for each tendon were similar.

3.3 Morphometric Analysis

3.3.1 Anatomical Measurements

The following muscles and tendons were dissected from the hind limbs of all 35 specimens listed above; digital flexors (plantaris, deep digital flexors [flexor hallucis and flexor digitorum longus]), ankle extensors (gastrocnemius and soleus [if present]), and common digital extensors. As there were no appreciable differences between left and right hind limbs in any of the specimens, the data from both hind limbs were pooled and averaged to represent one data point for each figure. In cases where only one hind limb was available, data points represent measurements from only that limb.

The effective length of the tendon can be difficult to determine as muscle and tendon shape and orientation differ from muscle to muscle and from species to species. In order to simplify this measurement the definition originally given

by Alexander (1974) was adopted (see figure 3.1). The effective length of the tendon on this basis is

$$L_t = (D - L_m) \quad (3.5)$$

where D is the overall length from origin to insertion and L_m is the length of the muscle fibres when the muscle belly is straight but under no tension.

The tendons were dissected from their muscle bellies, wrapped in plastic film and stored at -20°C until needed for mechanical testing. The mass of each muscle (M_m) was determined immediately after removal of the tendon. The muscles were fixed in a 20% formalin solution for 24 hours or more and then rinsed in water. Sections of muscle were cut in the plane of the fibres and fibre length measured with calipers. This procedure was used because several of the muscles are pennate, with short fibres, making it difficult to measure fibre length accurately in fresh material. Without establishing the sarcomere length of each fibre, this method has a possible uncertainty of up to 25% (due to the range of lengths over which muscle fibres operate) (Ker et al., 1988; Shadwick, 1990). From the muscle mass and fibre length data the muscle fibre cross-sectional area was calculated as

$$A_m = M_m / L_m \cdot \rho_m \quad (3.6)$$

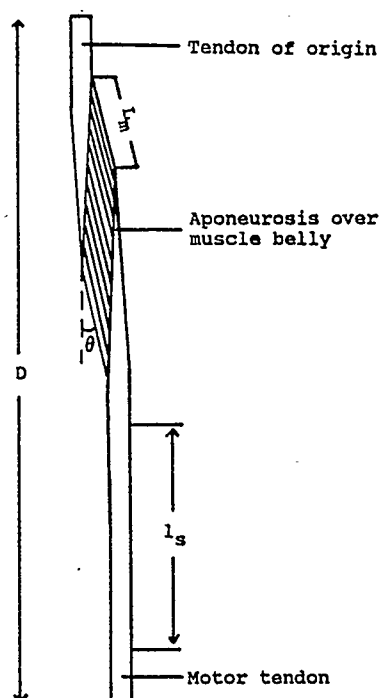


Figure 3.1. A diagrammatic view of a uni-pennate muscle tendon combination. The effective length of the tendon is $D - L_m$, where D is the overall length from origin to insertion and L_m is the length of the muscle fibres. This assumes the numeric value of $\cos \theta$ to be very close to one, where θ is the angle of pinnation. l_s represents length of selected portion of tendon for tensile tests (re-drawn from Ker et al., 1988).

This approximates the density of muscle as 1.06 g/cm^3 (Mendez and Keyes, 1960). Muscle fibre cross-sectional area calculations are prone to the same possible uncertainty as mentioned above for the fibre lengths (Ker et al., 1988; Shadwick, 1990).

The deep digital flexor and gastrocnemius are each made up of more than one muscle belly, so the mass (M_m) and cross-sectional area (A_m) given for each of these is the sum of the masses and fibre areas of the constituent muscle bellies for that particular muscle. This follows the

procedure outlined by Alexander et al., (1981). For a compound (multi-bellied) muscle of which the j th member has mass m_j and fibres of length l_j , the cross-sectional area of the muscle fibres (a_j) was calculated as follows:

$$a_j = m_j / l_j \cdot \rho_m \quad (3.7)$$

This gives the cross-sectional area of the muscle fibres for each constituent belly of the compound muscle. As well, each belly of the gastrocnemius and deep digital flexors may have very different fibre lengths, so in determining the muscle fibre length, L_m , for a compound muscle, the weighted harmonic mean fibre length was determined as

$$L_m = \Sigma m_j / \Sigma (m_j / l_j) \quad (3.8)$$

Immediately following biomechanical testing, measured lengths, l_s , were cut from tendons and their mass, m_s , determined. In a fashion similar to the method of determination of muscle fibre cross-sectional area, tendon cross-sectional area was determined by dividing the wet weight of a tendon sample by its length and density (equation 3.2).

3.3.2 Mechanical Parameters

As the peak isometric stress (force/cross-sectional area) of striated muscle appears to be relatively constant

among vertebrates (Wells, 1965; Close, 1972), at $\sigma_m \approx 0.3$ MPa, maximum muscle force can be estimated from the cross-sectional area of the muscle fibres [multiplied by the cosine of the angle of pinnation]. The angle of pinnation, θ , (Fig. 3.1) was never found to be greater than 30° and ranged more commonly from 10° to 25° , thus making $\cos \theta$ almost equal to 1 ($\cos 0^\circ = 1$; $\cos 30^\circ = 0.87$). Thus, the factor $\cos \theta$ was eliminated from the fibre area calculations, and hence muscle force estimation.

Since tendons are in series with their muscles, the maximum tension in a tendon cannot exceed the peak load ($F_m = \sigma_m A_m$) developed by the muscle. Therefore the maximal in vivo tendon stress (σ_t) is proportional to the ratio of the muscle and tendon cross-sectional areas, A_m/A_t and the maximal muscle stress (Ker et al., 1988), and is calculated as:

$$\sigma_t = 0.3 \text{ MPa}(A_m/A_t) \quad (3.9)$$

The factor of safety of a structure or component is the ratio of the load which would cause it to fail (ultimate strength), to the maximum load it is required to withstand (maximum tendon stress) (Alexander, 1981). Safety factors for the tendons were estimated by dividing the value for ultimate tendon strength (100 MPa (Bennett et al., 1986)) by the calculated values for maximum tendon stress.

The calculation of the following two parameters, length factor and elastic strain energy, employs the data obtained from both the mechanical tests and morphometric analysis. Since material properties for all tendons tested appear to be similar and independent of body mass, a typical stress-strain curve (Fig 4.1) was used to determine the maximal in vivo strain ($\dot{Y}_t$), which corresponds to the maximal in vivo tendon stress ($\dot{I}_t$). Tendon extension (ΔL_t) at maximal stress will be proportional to tendon strain and length as:

$$\Delta L_t = \dot{Y}_t L_t \quad (3.10)$$

The dimensionless fibre length factor, L , is defined as the ratio of muscle fibre length to the extension of the tendon when the muscle is maximally contracted ($\dot{I}_m \sim 0.3$ MPa) and expresses the relative importance of muscle and tendon length changes under these conditions (Ker et al., 1988). This parameter can be used to determine whether a muscle-tendon unit favors elastic energy storage ($L < 2$) or control of joint displacement and minimal total mass ($L > 4$) (Ker et al., 1988; Shadwick, 1990).

When an elastic material deforms reversibly, the product of stress and strain gives energy, U . In this case (cyclic tensile testing) strain energy can be approximated as the area under the linear portion of the stress strain curve. Strain energy is calculated as, $U = 1/2 \dot{I} \dot{Y}$, per unit volume of material, having units of Joules/m³

(Wainwright et al., 1976). In an intact animal, however, the storage capacity of elastic strain energy depends upon the level of in vivo tendon stress and strain. Again, combined with data from morphometric analysis and tensile tests, an estimate of the maximal in vivo stress and strain was used to calculate the corresponding maximum capacity for storage of elastic strain energy, as follows:

$$U = [1/2(\sigma_t \cdot \epsilon_t)] [L_t \cdot A_t] \quad (3.11)$$

having units of Joules.

Allometric equations for each variable listed in Tables 4.2 - 4.4 were obtained by least squares regression after transformation of the variables X and Y to logarithms. Body mass (X) was treated as the independent variable. The allometric equations are reported in the form $Y = a X^b$. Untransformed data were plotted on log-log scaled graphs (Schmidt-Nielsen, 1984; Peters, 1983). A Student's t test and standard error calculation of the slope were used to assign 95% confidence limits to the allometric exponent, b (Zar, 1984). The correlation coefficient (r) for each equation was also calculated. The last step in the statistical analysis of the data involved applying analysis of co-variance tests (Zar, 1984), to determine whether the slopes (allometric exponents, b) or elevations (proportionality coefficients, a) of the allometric equations of each muscle and/or tendon unit were similar.

CHAPTER 4

RESULTS

4.1 Material Properties of Tendons

4.1.1 Stress-Strain curves

A typical cyclic stress strain curve is shown in figure 4.1. All tendons tested, whether they functioned primarily as ankle extensors, digital flexors or extensors, yielded similar J-shaped curves. Continued elongation resulted in a stiffening of the tissue, eventually resulting in a linear curve, beginning at approximately 20 - 35 MPa for most tendons. The elastic modulus was calculated as the slope of the linear portion of the loading curve. As long as the tendon was not extended beyond the linear region of the stress-strain curve, cyclic loading produced an elastic response, i.e., unloading restored the tendon to its original length. Hysteresis is represented by the area (A) enclosed by the loop. After a few conditioning cycles, the curves became quite stable. The average elastic modulus and mechanical hysteresis (from 2 - 8 cycles) was then determined for each tendon. These averaged values of elastic modulus and hysteresis for each tendon were used in the allometric equation calculations.

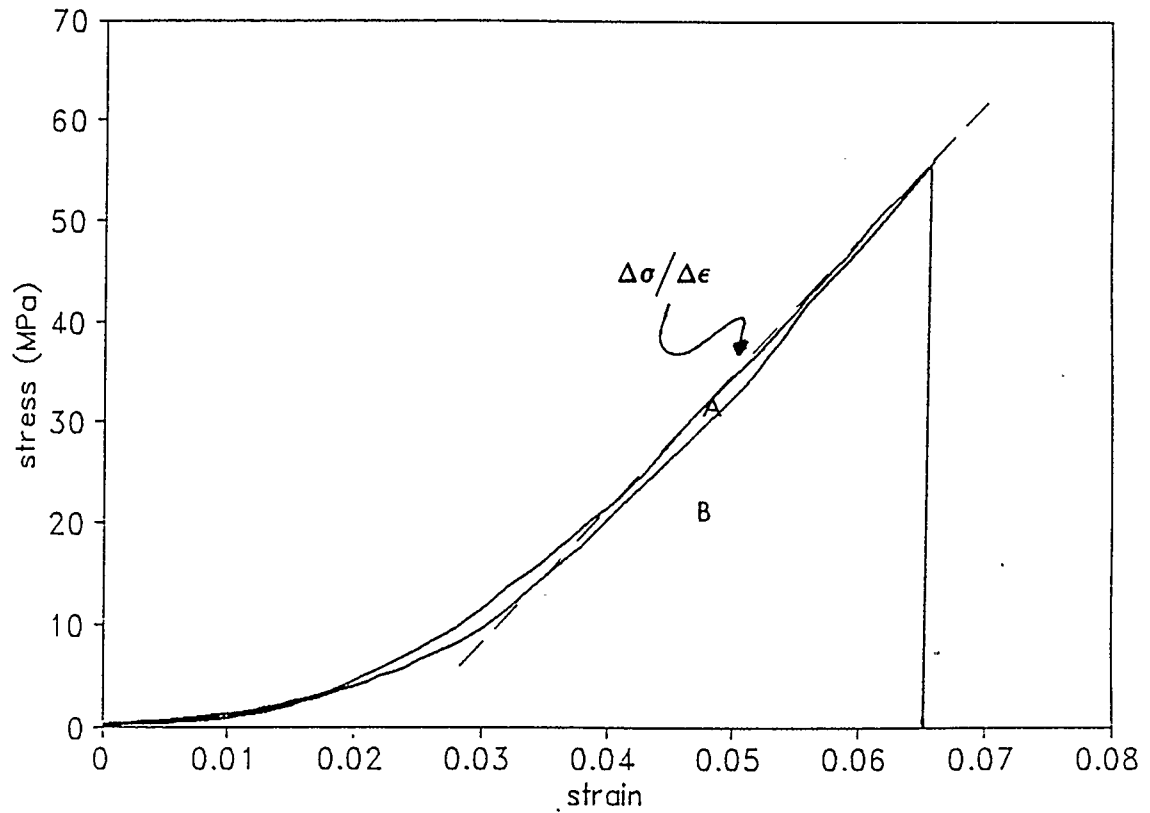


Figure 4.1. A typical stress strain curve for a mammalian tendon. Arrows on the curve indicate the direction of loading. Elastic modulus is calculated as the slope ($\Delta\sigma/\Delta\epsilon$) of the linear portion of the loading curve. Hysteresis (represented by area A) is 5.1% of the total strain energy input (area A+B).

4.1.2 Elastic Modulus and Hysteresis

The data show that in adult mammals, tendons associated with functionally different muscles, such as the ankle extensor, digital flexors and digital extensors are materially similar, and their material properties appear to be independent of body mass. Table 4.1 and Figs. 4.2 and 4.3 show that for each of the tendon types, both elastic modulus (E_t) and hysteresis (H_t) are neither body size nor species dependent. Modulus of elasticity ranged from approximately 0.9 to 1.8 GPa, with an average value of 1.24 (± 0.23) GPa for all tendon types. Hysteresis typically ranged from 3 to 20%, with an average value of 9.3 (± 5.0)% for all tendon types. Using Student's t test it was found that for all tendon types the scaling exponent, b , for both elastic modulus and hysteresis was not significantly different from zero ($P > 0.05$), indicating no dependence between these variables and body size. However, it should be noted that the hysteresis for the plantaris tendon appears to follow a decreasing trend with greater body mass (Fig 4.3), although this is not statistically significant.

Analysis of covariance applied to the elastic modulus data yields a common allometric exponent (b_c) of 0.00 and a common proportionality coefficient (a_c) of 1.22 for all tendon types tested, illustrated by the solid line in figure 4.2. Similarly, analysis of covariance applied to the hysteresis data yields a common scaling exponent (b_c) of -0.03 and a common proportionality coefficient (a_c) of 8.89

for all tendon types, illustrated by the solid line in figure 4.3. Further correlation coefficients (r), such as those in Table 4.1 (approaching zero), denote that there is no linear association between the magnitudes of the X and Y variables; that is, a change in magnitude in one does not imply a change in magnitude of the other (Zar, 1984)

4.2 Morphometric Analysis

4.2.1 Muscle Dimensions

The relationships of the muscle parameters (mass, fibre length and fibre cross-sectional area) to body mass are shown in figures 4.4 - 4.6. The corresponding allometric constants for non-hoppers only are listed in Table 4.2.

The allometric exponent, b , for muscle mass for all the muscles, (plantaris, deep digital flexors, gastrocnemius and common digital extensors) is not significantly different from a value of 1 ($P > 0.05$), indicating a simple proportionality, as expected for geometric scaling. Further, the correlation coefficients for each tendon are all greater than 0.97, indicating that the data from each category fall on a straight line and that there is a very strong positive linear association between the two variables (muscle mass and body mass). Analysis of co-variance applied to these four groups of data yields a common allometric exponent (b_c) of 0.98. The proportionality coefficients (a) for the four equations are, however,

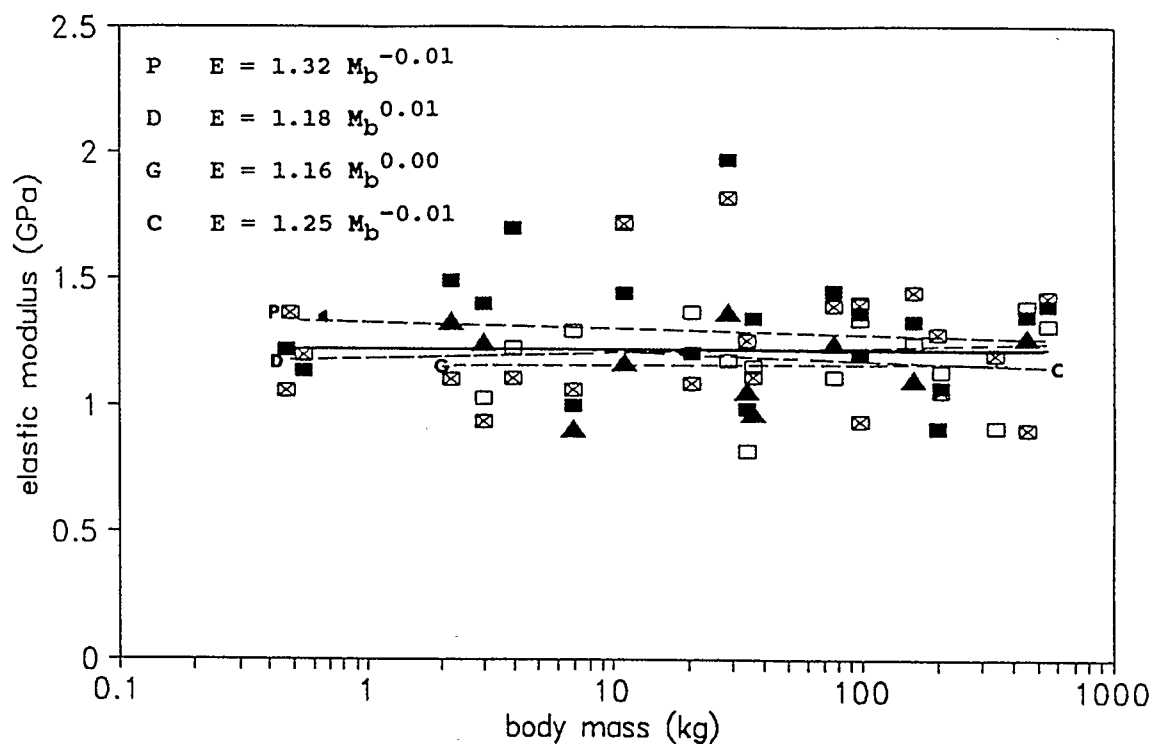


Figure 4.2. Semi-log plot of the relationship between tendon elastic modulus (E_t) in GigaPascals and body mass (M_b) in kilograms, for all tendons tested. The points for each tendon are represented by symbols and the dashed regression lines are labelled by letters, as follows: ■ P, plantaris; ☒ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensor. The common regression line is represented by the solid line. Allometric equations for each tendon are listed in the upper left hand corner.

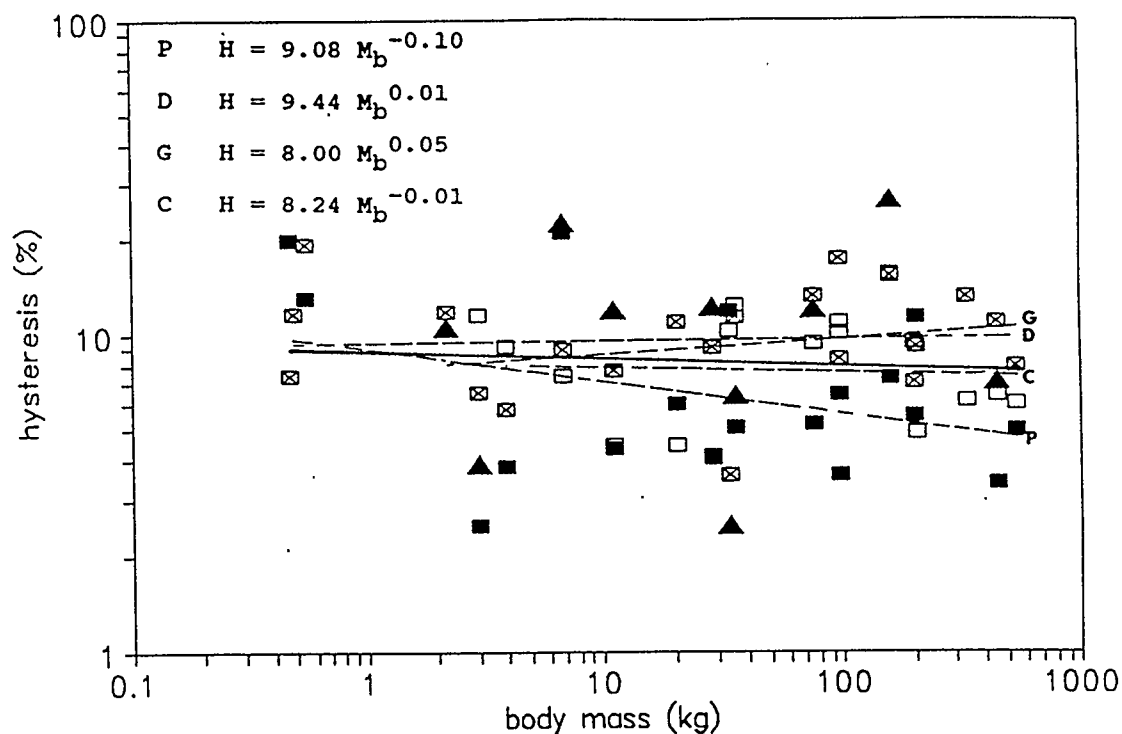


Figure 4.3. Log-log plot of the relationship between tendon mechanical hysteresis (H_t) and body mass (M_b) in kilograms for all tendons tested. The points for each tendon are represented by symbols and the dashed regression lines are labelled by letters, as follows: ■ P, plantaris; ☒ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensor. The common regression line is represented by the solid line. Allometric equations for each tendon are listed in the upper left hand corner.

Table 4.1. Analysis of mechanical data for non-hoppers only. Values of allometric parameters for $Y=aX^b$, where Y is the dependent variable listed and X is body mass (M_b) in kg. The equations were determined by least squares regression after logarithmic transformation. N refers to the number of specimens (body weights) used in each category. 95% confidence intervals (CI) of the allometric exponent (b), and the correlation coefficients (r) are also included. Analysis of co-variance revealed common regression (b_c) and proportionality coefficients (a_c). Therefore, the entire data set for each variable, Y, can be represented by the common allometric equation listed.

TENDON	N	a	b	95% CI	r
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ELASTIC MODULUS (GPa)

PLA	19	1.32	-0.01	0.04	-0.09
DDF	21	1.18	0.01	0.04	0.09
GAS	10	1.16	0.00	0.06	0.00
CDE	17	1.25	-0.01	0.06	-0.11

COMMON ALLOMETRIC EQUATION $Y = 1.22 X^{0.00}$

HYSTERESIS (%)

PLA	18	9.08	-0.10	0.14	-0.36
DDF	21	9.44	0.01	0.08	0.03
GAS	10	8.00	0.05	0.34	0.11
CDE	17	8.24	-0.01	0.13	-0.06

COMMON ALLOMETRIC EQUATION $Y = 8.89 X^{-0.03}$

significantly different from one another. When the numerical value of the exponents (b) in the allometric equations are the same, the proportionality coefficients (a) can be used directly to compare the magnitude of the variable in question (Schmidt-Nielsen, 1984). These proportionality coefficients show that for mammals in general (excluding bipedal hoppers) the muscle mass of the gastrocnemius is a little more than two and one half times that of each of the plantaris and deep digital flexors, and about seven and one half times that of the common digital extensors.

Close inspection of figure 4.4 reveals that the muscle masses for the plantaris and gastrocnemius of the kangaroo rats and the plantaris of the wallaby greatly exceed what would be predicted for their respective body masses based upon allometric equations derived from the non-hoppers.

The allometric exponent, b , for fibre length of each muscle (plantaris, deep digital flexor, gastrocnemius and common digital extensor) is significantly different from that predicted by geometric scaling, i. e., $b = 0.33$ ($P < 0.001$). As well, fibre lengths unlike muscle mass, do not show the same trend for all muscle types. The scaling exponent, b , for the deep digital flexors, gastrocnemius and common digital extensors ranges from 0.18 - 0.24, with a common exponent (b_c) of 0.21. The scaling exponent is, however, much lower for the plantaris ($b=0.05$), as well as being not significantly different from zero ($P > 0.05$).

This is, in part, due to the very short plantaris muscle fibres of some ungulates. There is a very low correlation coefficient (0.23), again indicating very little association between the magnitudes of X (body mass) and Y (plantaris fibre length).

The scaling exponents of the calculated total muscle fibre cross-sectional areas for plantaris and deep digital flexors are statistically similar ($P > 0.05$). Analysis of covariance yields a common scaling exponent (b_C) of 0.88 and a common proportionality coefficient (a_C) of 129.4, indicating that there is no significant difference between plantaris and deep digital muscle fibre cross-sectional areas. All the allometric exponents for fibre area, with the exception of that for the digital extensors, are significantly greater ($P < 0.001$) than that predicted by geometric scaling. The higher scaling exponent for the digital flexors and ankle extensors compared to the digital extensors is due to the relatively shorter fibres found in the plantaris, deep digital flexor and gastrocnemius muscles. The correlation coefficients are again very large, indicating a strong positive correlation between body mass and each of the muscle fibre areas. Assuming maximum muscle force per unit area (stress) is constant, the plantaris, deep digital flexors and gastrocnemius muscles, due to their greater fibre cross-sectional areas, are able to exert much greater forces than the muscles of the common digital extensors for any body mass.

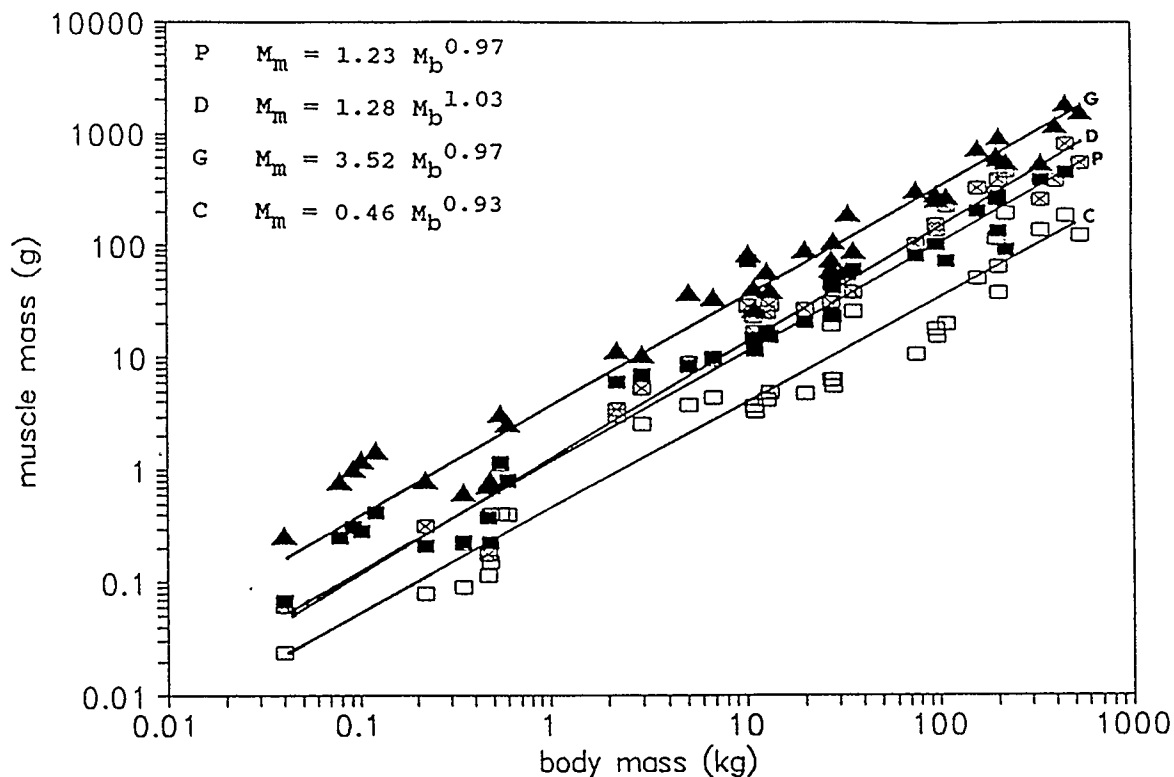


Figure 4.4. Log-log plot of the relationship between muscle mass (M_m) in grams and body mass (M_b) in kilograms for four muscles. Muscle mass increases in direct proportion to body mass for all muscles studied. The points for each muscle are represented by symbols and the regression lines are labelled by letters, as follows: ■ P, plantaris; ⊠ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensors. Allometric equations for each muscle are listed in the upper left hand corner.

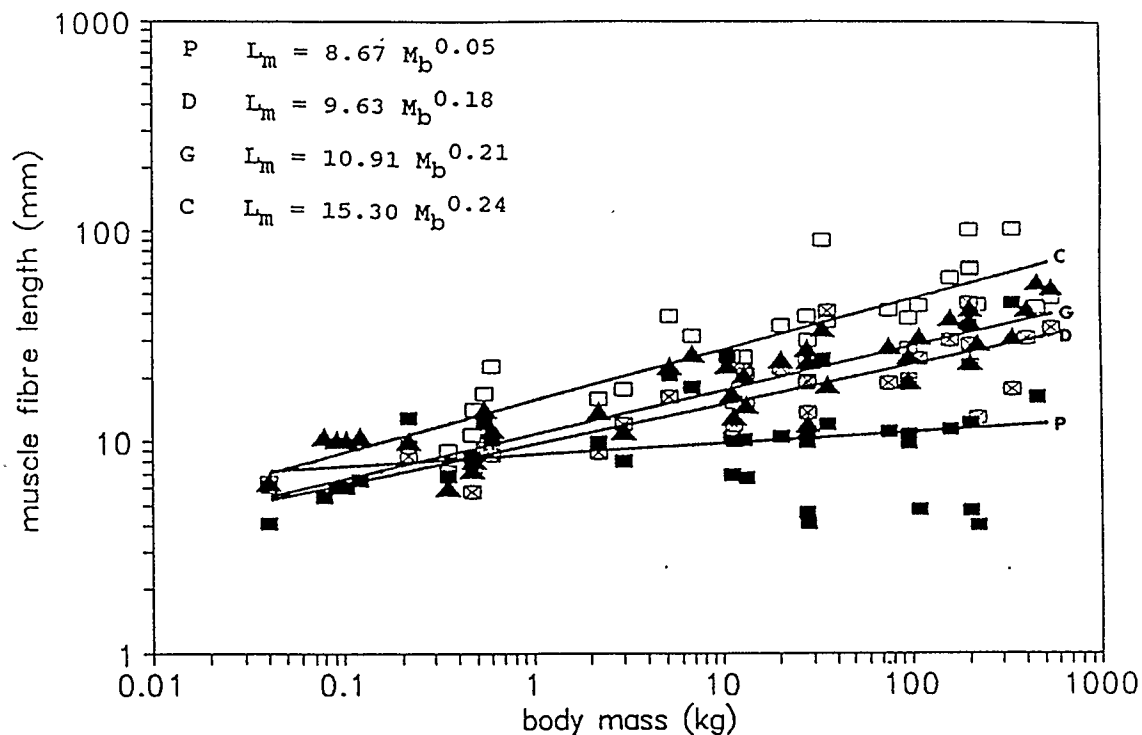


Figure 4.5. Log-log plot of the relationship between muscle fibre length (L_m) in millimeters and body mass (M_b) in kilograms for four muscles. Note that the extremely short fibered plantaris in some ungulates markedly affects the slope of the regression line for this muscle. The points for each muscle are represented by symbols and the regression lines are labelled by letters, as follows: ■ P, plantaris; ☒ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensors. The allometric equations for each muscle are listed in the upper left hand corner.

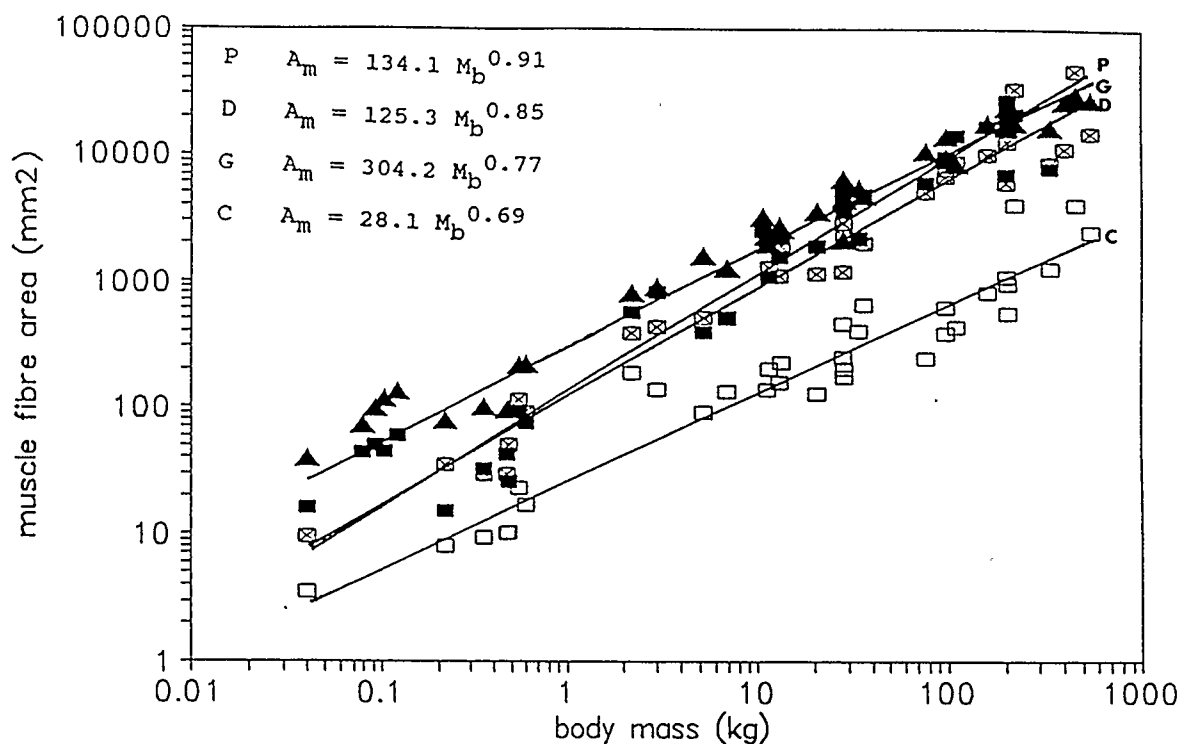


Figure 4.6. Log-log plot of the relationship between muscle fiber cross-sectional area (A_m) in mm^2 and body mass (M_b) in kilograms for four muscles. Since the maximum isometric stress (force/area) that can be produced by striated muscle (0.3 MPa) is standard for vertebrates (Wells, 1965; Close, 1972), the muscle force can be estimated from the total cross-sectional area of the muscle fibers. The points for each muscle are represented by symbols and the regression lines are labelled by letters, as follows: ■ P, plantaris; ▲ D, deep digital flexors; ● G, gastrocnemius; □ C, common digital extensors. The allometric equations for each muscle are listed in the upper left hand corner.

Table 4.2. Morphometric analysis of muscle anatomical data for non-hoppers only. Values of allometric parameters for $Y=aX^b$, where Y is the dependent variable listed and X is body mass (M_b) in kg. The equations were determined by least squares regression after logarithmic transformation. N refers to the number of specimens (body weights) used in each category. 95% confidence intervals (CI) of b, and correlation coefficients (r) are also included.

MUSCLE	N	a	b	95% CI	r
MUSCLE MASS (g)					
PLA	33	1.23	0.97	0.06	0.98
DDF	35	1.28	1.03	0.05	0.99
GAS	35	3.52	0.97	0.06	0.99
CDE	34	0.46	0.93	0.08	0.97
MUSCLE FIBER LENGTH (mm)					
PLA	33	8.67	0.05	0.08	0.23
DDF	35	9.63	0.18	0.04	0.86
GAS	35	10.91	0.21	0.04	0.87
CDE	34	15.30	0.24	0.05	0.87
MUSCLE FIBER CROSS-SECTIONAL AREA (mm ²)					
PLA	33	134.10	0.91	0.08	0.97
DDF	35	125.28	0.85	0.06	0.98
GAS	35	304.17	0.77	0.04	0.99
CDE	34	28.09	0.69	0.08	0.96

Similar to the trend for muscle mass, the muscle fibre area for the plantaris and gastrocnemius of the kangaroo rats and plantaris of the wallaby are larger than would be predicted for their respective body masses based on allometric equations derived from non-hoppers.

4.2.2 Tendon Dimensions

The relationships between the tendon parameters (cross-sectional area and length) and body mass are illustrated in figures 4.7 and 4.8. The corresponding allometric constants for non-hoppers only are listed in Table 4.3.

The scaling exponent, b , for the tendon cross-sectional area of the plantaris, deep digital flexors and gastrocnemius, are statistically similar as well as being not significantly different from that predicted by geometric scaling ($P > 0.05$). Analysis of co-variance yields a common allometric exponent, b_c , of 0.67. The differing proportionality coefficients indicate that for mammals in general (excluding bipedal hoppers) the combined tendon area of the deep digital flexors is almost twice that of the plantaris. The allometric exponent for the common digital extensor tendon area, however, is significantly lower at 0.56 ($P < 0.005$).

Figure 4.7 reveals that the tendon cross-sectional area of the kangaroo rats' plantaris and gastrocnemius and the wallaby's plantaris are considerably larger than would have been predicted for their respective body masses based on

allometric equations derived from non-hoppers.

The allometric exponents for tendon length are both statistically similar to one another and not significantly different than that predicted by geometric scaling ($P > 0.05$). The common scaling exponent, b_c , is 0.35 for all tendons considered. The proportionality coefficients, a , indicate the relative length of each tendon. The allometric exponents for both the tendon cross-sectional area and tendon length are considered reliable, since the correlation coefficients for each equation are very high.

4.3 Muscle-Tendon Parameters

The relationships for the muscle-tendon parameters (area ratio, length factor and capacity for storage of elastic strain energy) are illustrated in figures 4.9 - 4.11. The corresponding allometric constants for non-hoppers only are listed in Table 4.4.

The allometric exponents for muscle/tendon area ratio of the plantaris, deep digital flexors, gastrocnemius and common digital extensor are all significantly larger than that predicted by geometric scaling ($P < 0.05$). The scaling exponents of the muscle/tendon area ratio (A_m/A_t) for the deep digital flexors and plantaris are considerably larger (0.21 - 0.24) than those of the gastrocnemius and common digital extensors (0.08 - 0.13). The corresponding common scaling exponents are $b_c=0.22$ and $b_c=0.10$, respectively.

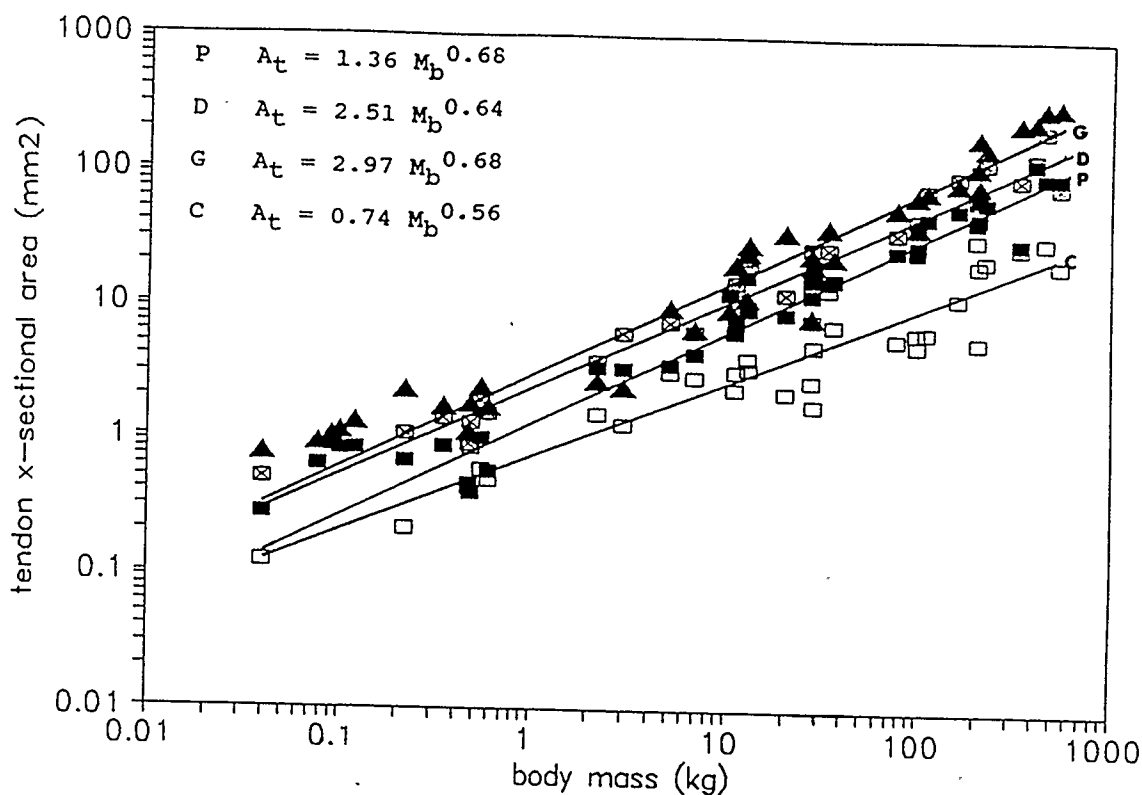


Figure 4.7. Log-log plot of the relationship between tendon cross-sectional area (A_t) in mm² and body mass (M_b) in kilograms for four tendons. The points for each tendon are represented by symbols and the regression lines are labelled by letters, as follows: ■ P, plantaris; ▣ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensors. Arrows point out the tendon cross-sectional areas of the kangaroo rats' plantaris and gastrocnemius and the wallaby's plantaris. The allometric equations for each tendon are listed in the upper left hand corner.

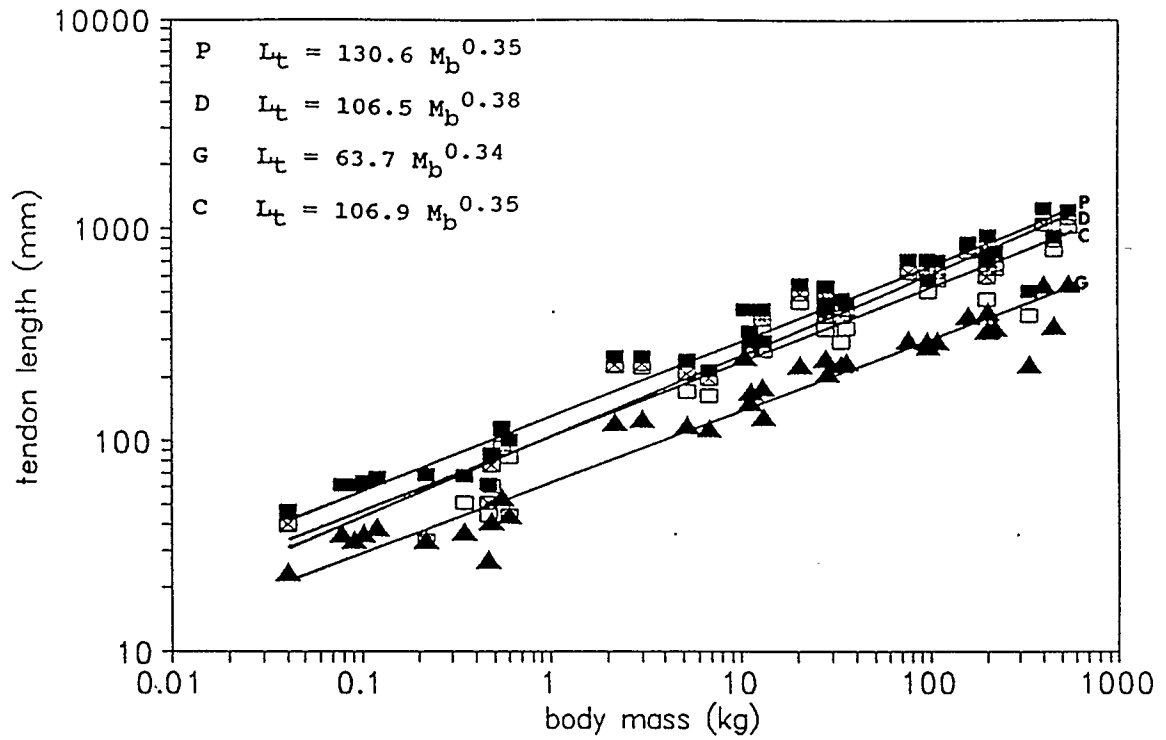


Figure 4.8. Log-log plot of the relationship between tendon length (L_t) in millimeters and body mass (M_b) in kilograms for four tendons. The points for each tendon are represented by symbols and the regression lines are labelled by letters, as follows: ■ P, plantaris; ■ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensors. The allometric equations for each tendon are listed in the upper left hand corner.

Table 4.3. Morphometric analysis of tendon anatomical data for non-hoppers only. Values of allometric parameters for $Y=aX^b$, where Y is the dependent variable listed and X is body mass (M_b) in kg. The equations were determined by least squares regression after logarithmic transformation. N refers to the number of specimens (body weights) used in each category. 95% confidence intervals (CI) of b, and correlation coefficients (r) are also included.

TENDON	N	a	b	95% CI	r
TENDON CROSS-SECTIONAL AREA (mm ²)					
PLA	35	1.36	0.68	0.04	0.98
DDF	35	2.51	0.64	0.04	0.98
GAS	34	2.97	0.68	0.07	0.97
CDE	33	0.74	0.56	0.07	0.95
TENDON LENGTH (mm)					
PLA	35	130.56	0.35	0.03	0.97
DDF	35	106.54	0.38	0.04	0.96
GAS	35	63.72	0.34	0.03	0.97
CDE	34	106.87	0.35	0.04	0.95

From equation 3.9, if the area ratio values are multiplied by the constant maximum muscle stress, 0.3 MPa, this would produce resultant maximal in vivo tendon stresses with scaling exponents following the same trends as the area ratios seen in Fig. 4.9 and Table 4.4. The proportionality coefficient (a) for the plantaris area ratio is twice as large as that of the deep digital flexors, therefore, the plantaris tendon would experience twice the maximum in vivo stress as that of the deep digital flexors. Despite the fact that the gastrocnemius muscle is capable of exerting much greater forces than the common digital extensor, due to the robustness of their respective tendons, the tendon of the gastrocnemius experiences only two and one half times the maximum in vivo stress of that of the common digital extensors.

Of the bipedal hoppers only the area ratio of the wallaby's gastrocnemius muscle-tendon unit is greatly different (being more than twice as large) from what would have been predicted based on the allometric constants in Table 4.4.

The length factor (L) is proportional to the ratio of muscle fibre length and tendon extension at maximum muscle stress (0.3 MPa). The length factors for the plantaris and deep digital flexors decrease with increasing body size at a greater rate than those of the gastrocnemius and common digital extensors. This is indicated by the scaling exponents of the digital flexors being more negative than

those of the ankle and digital extensors. The scaling exponents for the length factors of the gastrocnemius and digital extensors are statistically similar ($P > 0.05$). However, as indicated by their respective proportionality coefficients, the gastrocnemius is designed for a lower value of L than are the digital extensors for all body sizes.

Again, of the bipedal hoppers, only the length factor for the wallaby's gastrocnemius muscle-tendon unit is different (being much lower) from what would have been predicted for its body mass based on allometric constants in Table 4.4.

The scaling exponents of the capacity for elastic strain energy storage for all the tendons is greater than one. Supported by very high (>0.95) correlation coefficients, this indicates that the capacity for storage of elastic strain energy increases at a greater rate than increases in body mass. Thus, larger mammals have a greater capacity for storage of elastic strain energy than do smaller mammals. Even though the exponents are all greater than one, the exponent for the common digital extensors is not significantly different from one ($P > 0.05$). Thus the capacity for storage of elastic strain energy increases more rapidly with increasing body mass in those tendons that experience greater stresses (digital flexors and ankle extensors), when compared to tendons that do not experience such large stresses (digital extensors).

As far as the tendons of the bipedal hoppers are concerned, they are capable of storing as much elastic strain energy as would be predicted for their respective body masses, with the exception of the kangaroo rats' plantaris and the wallaby's gastrocnemius tendons, which are capable of storing much more energy than would have been predicted from the allometric constants in Table 4.4.

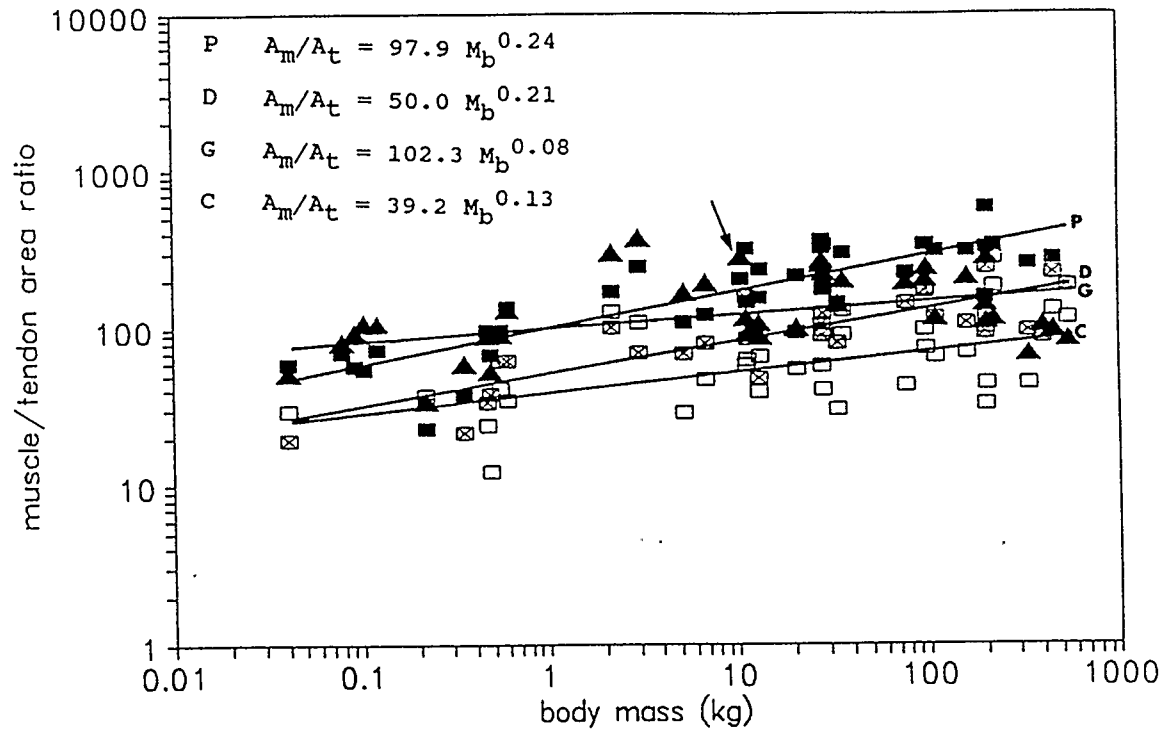


Figure 4.9. Log-log plot of the relationship between the muscle/tendon area ratio (A_m/A_t) and body mass (M_b) in kilograms for four muscle-tendon combinations. Since tendons are in series with their muscles, the maximum tendon tension cannot exceed the load developed by its muscle. Therefore the maximum tendon stress (σ_t) is proportional to the ratio of muscle and tendon cross-sectional areas. The points for each muscle-tendon unit are represented by symbols and regression lines are labelled, as follows: ■ P, plantaris; ⊠ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensors. The arrow points out the wallaby's gastrocnemius muscle/tendon area ratio. The allometric equations for each muscle-tendon unit are listed in the upper left hand corner.

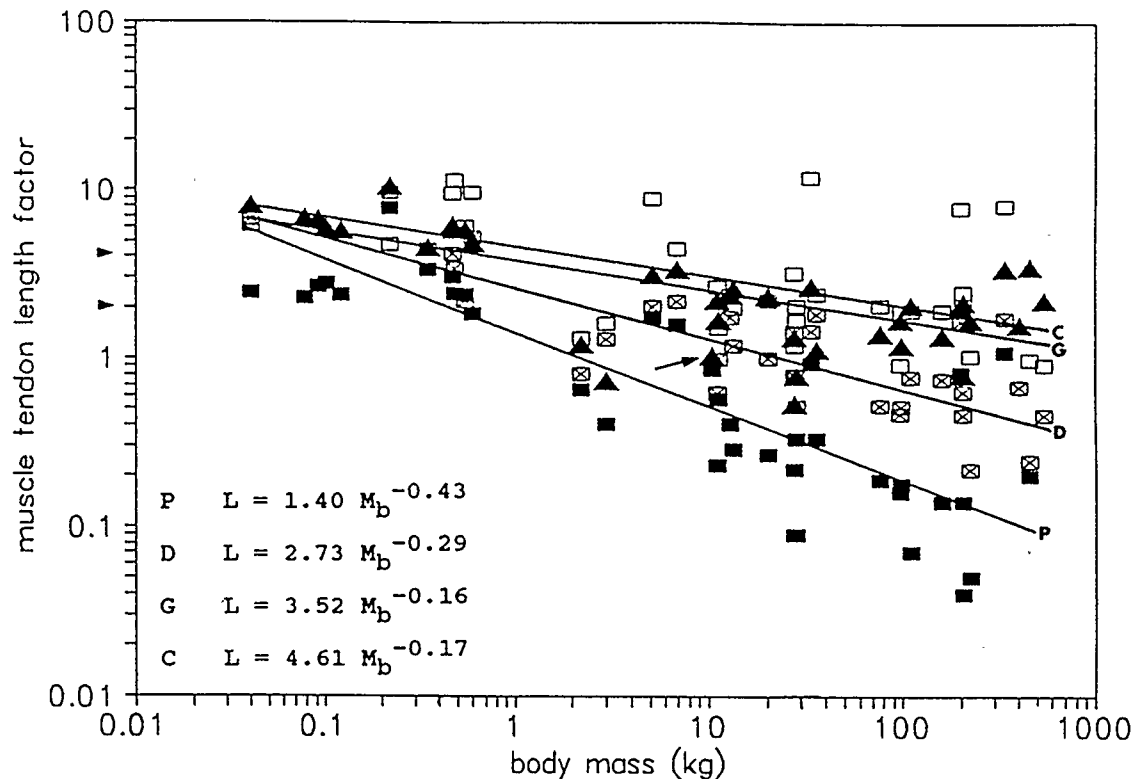


Figure 4.10. Log-log plot of the relationship between the length factor (L) and body mass (M_b) in kilograms for four muscle-tendon combinations. The area between values of $L < 4$, but > 2 demarcates a transition zone between a design for elastic energy storage ($L < 2$) versus control for joint displacement ($L > 4$). Due to their low values for L the plantaris, deep digital flexor and gastrocnemius muscle-tendon unit of large mammals appears to be more suited for elastic energy storage. The points for each muscle-tendon unit are represented by symbols and regression lines are labelled by letters, as follows: ■ P, plantaris; ▣ D, deep digital flexors; ▲ G, gastrocnemius; □ C, common digital extensors. The arrow points out the length factor for the wallaby's gastrocnemius. The allometric equations for each muscle-tendon unit are listed in the lower left hand corner.

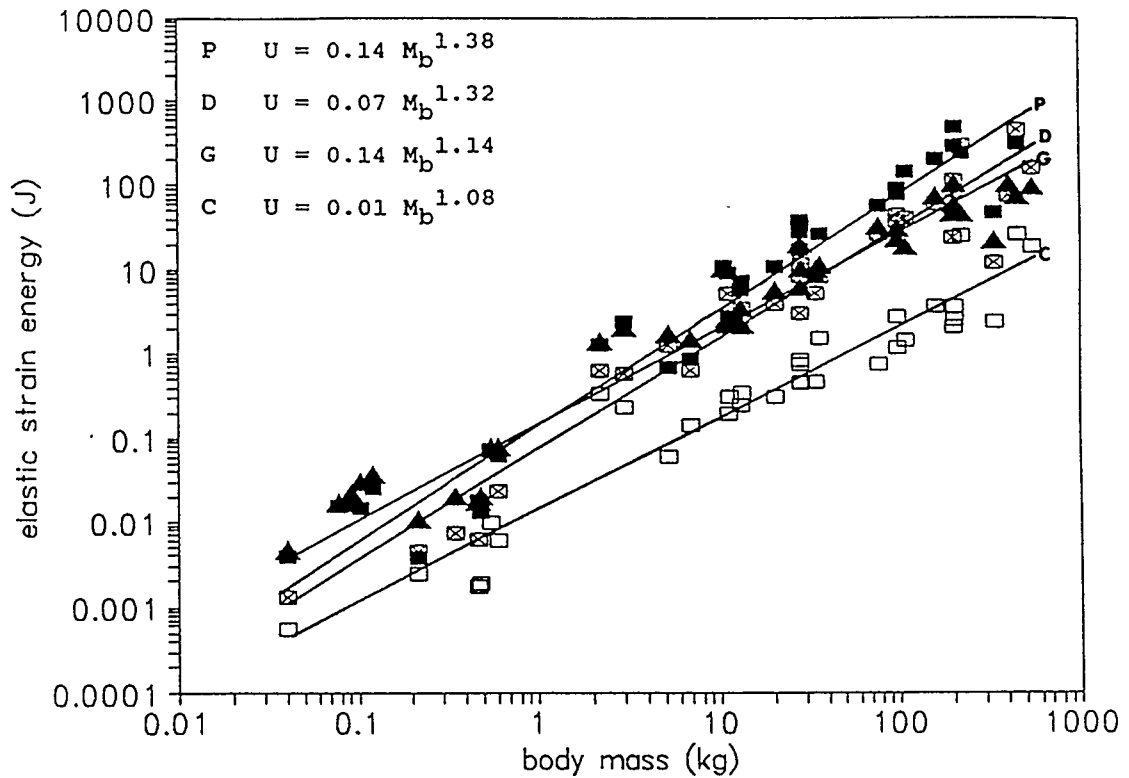


Figure 4.11. Log-log plot of the relationship between the maximum capacity for elastic strain energy storage (U) in Joules and body mass (M_b) in kilograms for four tendons. Since U scales with an exponent greater than one, the capacity for elastic strain energy is greater in large mammals, especially in tendons that experience larger stresses. The points for each tendon are represented by symbols and regression lines are labelled by letters, as follows: ■ P, plantaris; ▣ D, deep digital flexors, ▲ G, gastrocnemius; □ C, common digital extensors. The allometric equations for each tendon are listed in the upper left hand corner.

Table 4.4. Morphometric analysis of muscle/tendon anatomical data for non-hoppers only. Values of allometric parameters for $Y=aX^b$, where Y is the dependent variable listed and X is body mass (M_b) in kg. The equations were determined by least squares regression after logarithmic transformation. N refers to the number of specimens (body weights) used in each category. 95% confidence intervals (CI) of b, and correlation coefficients (r) are also included.

MUSCLE/TENDON	N	a	b	95% CI	r
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MUSCLE/TENDON AREA RATIO

PLA	33	97.94	0.24	0.06	0.82
DDF	35	49.98	0.21	0.05	0.83
GAS	34	102.30	0.08	0.07	0.37
CDE	33	39.15	0.13	0.07	0.53

LENGTH FACTOR

PLA	33	1.40	-0.43	0.13	-0.78
DDF	35	2.73	-0.29	0.07	-0.82
GAS	34	3.52	-0.16	0.08	-0.59
CDE	33	4.61	-0.17	0.10	-0.52

ELASTIC STRAIN ENERGY (Joules)

PLA	32	0.14	1.38	0.13	0.97
DDF	35	0.07	1.32	0.11	0.97
GAS	34	0.14	1.14	0.10	0.97
CDE	33	0.01	1.08	0.12	0.96

CHAPTER 5

DISCUSSION

5.1 Material Properties of Tendons

5.1.1 Stress-Strain Curves

The J-shaped stress-strain curves obtained in this study, whether they were from tendons of ankle extensors, digital extensors or digital flexors are typical of those previously reported for mammalian tendons. The initial concave portion of the curve is believed to be the result of a structural change in fibril organization from a crimped, wavy pattern to a more parallel arrangement (Butler et.al., 1978; Viidik, 1980). With continued elongation (increased stresses) the slope of the stress-strain curve (i.e., elastic modulus) does not significantly change and the curve becomes linear (Fig 4.1). Elastic modulus in this region of the curve represents the elastic stiffness of the straightened collagen fibre bundles (Viidik, 1980). Previous studies show uniformity in tendon stiffness is typically attained at stresses beginning at 17 to 30 MPa (Ker, 1981; Dimery and Alexander, 1985; Bennett et al., 1986). Similar to previous studies, the results of the tensile tests in this study show that the stress-strain curve becomes linear as stresses approach 20 to 35 MPa. One must ask, however, whether these levels of tendon stresses

are realistically attained during mammalian locomotion. The answer is yes; the in vivo stresses ankle extensor and digital flexor tendons typically experience during moderate to fast running and jumping, (Table 5.1) are sufficient to stretch the tendon so that it enters the linear region of its stress-strain curve.

5.1.2 Elastic Modulus and Hysteresis

Two new major findings have resulted from the tensile tests carried out in this study. Firstly the digital flexor and ankle extensor tendons (those likely to act as springs during the support phase of locomotion) have been demonstrated to have the same material properties (ie., elastic modulus and hysteresis) as the digital extensors (those not likely to function as springs). Secondly, the material properties of these functionally different tendons are neither species or body size dependent (Figs 4.2 & 4.3; Table 4.1). For all tendon types tested, the mean elastic modulus value is 1.24 (± 0.23) GPa, and the mean hysteresis value is 9.3 (± 5.0)%.

These results are in agreement with those of Bennett et al., (1986), who found no consistent differences in material properties (elastic modulus, percent energy dissipation (hysteresis) and ultimate strength) for tendons from different anatomical sites and different species. Elastic modulus averaged 1.5 GPa (at stresses above 30 MPa), hysteresis ranged from 6 to 11% and ultimate strength ranged

Table 5.1. Peak in vivo stresses calculated for ankle extensor or digital flexor tendons during moderate to fast locomotion. Asterisk (*) indicates corrected stress values; original published values are slightly higher, as an incorrect value for tendon density was used (see Ker et al., 1986)

	Tendon Stress MPa	Literature Source
Wallaby hopping	15 - 41	*Alexander & Vernon 1975; Ker et al., 1986
Kangaroo hopping	39 - 78	*Alexander & Vernon 1975
Dog jumping	84	*Alexander, 1974
Camel pacing	18	Alexander et al., 1982
Deer galloping	28 - 74	Dimery et al., 1986
Donkey trotting	28 - 37	Dimery & Alexander, 1985
Antelope galloping	27 - 51	*Alexander, 1977
Buffalo galloping	13 - 48	*Alexander, et al., 1979
Kangaroo rat hopping & jumping	10 - 36	Biewener & Blickhan, 1988

from 80 - 100 MPa. However, tendons tested in their study represented only those thought to function as elastic energy stores during locomotion (e.g. ankle extensors and digital flexors of terrestrial mammals and the sarcocaudalis of aquatic mammals). They suggested that other tendons associated with muscles of different functions may have different properties.

This study expands the sample set to include the digital extensor tendons, whose muscles are thought to be active during the swing phase of locomotion as opposed to the support phase, and can therefore be expected to experience less stress. The material properties of the digital extensors are no different from those of the digital flexors and ankle extensor tendons. Over a range of body mass from 0.5 to 545 kg, elastic modulus and hysteresis of functionally different tendons are constant, being independent of body mass.

These findings are in marked contrast to studies by Woo (1982) and Shadwick (1990). Results from both these studies show the digital flexor tendons of mature pigs to have higher elastic modulus (stiffer) and higher breaking stresses (stronger) than do digital extensor tendons at equivalent strains. This corresponds to a much higher capacity for storage of elastic strain energy in the tendons of the digital flexors. Shadwick (1990) postulated that the differences in material properties between these functionally distinct tendons are correlated with their

physiological functions: the highly stressed flexors, by being much stiffer, are much better suited to act as effective biological springs than are the extensors.

However, in a long term exercise study with similar pigs, Woo et al., (1980) showed that the tendons of digital extensors significantly increased in stiffness. In contrast, Woo et al. (1982) found that both short and long term exercise had no effect on the stress-strain curves (material properties) of the tendons of the digital flexors. The stress-strain curves generated from the tendons of the digital extensors and the digital flexors of pigs, after twelve months of exercise, are virtually the same (Woo et al., 1982). If the exercised pigs are taken to be equivalent to the adult wild animals in this study then there is no discrepancy in the results. The present study, with its large sample size, composed almost entirely of non-domesticated animals, clearly shows that the material properties of tendons associated with functionally distinct muscles are all the same in adult mammals. It appears that tendon is mechanically a highly conservative tissue, retaining constant material properties regardless of its function, anatomical location or the size of the organism. However, as the next section will show, digital flexors and ankle extensors are still more suited as biological springs, not because their tendons are stiffer than those of digital extensors, but because their muscles are able to exert

greater forces, thus stretching the tendons to a greater degree.

5.2 Morphometric Analysis

5.2.1 Muscle Dimensions

The general findings of the allometric analysis of muscle mass, fibre length and cross-sectional area (Figs. 4.4 - 4.6; Table 4.2), at least for the digital flexors and ankle extensors, are in accord with observations made by Alexander et al., (1981). To my knowledge, no previous studies have investigated the allometric relationships of these parameters for the digital extensors. The plantaris, deep digital flexor, gastrocnemius and common digital extensors of non-hoppers all have muscle masses directly proportional to body mass ($M_m \propto M_b^{0.98}$) (Table 4.1). For no muscle is the scaling exponent for muscle mass significantly different from 1, exhibiting what is predicted by geometric or isometric scaling (Appendix A).

Alexander et al., (1981) also noted that the muscle masses of bipedal hoppers are generally larger than homologous muscles found in non-hopping mammals of similar size. This might be expected, since the hind limbs of these mammals seem to have been enlarged at the expense of the forelegs.

Muscle fibre length for each muscle type scales with negative allometry; in other words, the allometric exponents

for L_m (Table 4.2) are less than those predicted by geometric scaling ($L_m \propto M_b^{0.33}$). This means that as body size increases the fibre lengths do not increase as much as if L_m scaled geometrically. The allometric exponent for plantaris muscle fibre length is very low ($b=0.05$), confirming the apparent independence of plantaris fibre length and body mass seen in figure 4.5. This is, in part, due to the extremely short muscle fibres (4-7mm) found in some of the larger ungulates.

The calculated muscle fibre cross-sectional areas for the digital flexors and ankle extensors (Table 4.2) scale in a positive allometric fashion, (i.e., the scaling exponent in each case is greater than that predicted by isometry, because muscle fibre length scales with negative allometry and muscle mass scales isometrically (Appendix A)). However, the muscle fibre cross-sectional area of the digital extensors scales isometrically and the allometric exponent is not significantly different from 0.67.

5.2.2 Muscle Force

As muscle fibres can develop constant peak stresses, the maximal forces they exert are therefore proportional to fibre cross-sectional area. At any body size, muscles with large cross-sectional areas, such as the digital flexors and ankle extensors, are consequently capable of exerting greater forces than muscles of the digital extensor group. The scaling exponents from muscle cross-sectional area

(Table 4.2) also predict that large mammals will have stronger digital flexor and ankle extensor muscles than if they were geometrically similar to small mammals. This is especially evident for some of the larger ungulates, whose extra muscle strength is due to unusually short fibres in muscles of normal mass.

The bipedal hoppers also have stronger plantaris and gastrocnemius muscles than would have been predicted for non-hoppers of equivalent mass. This, however, is due to them having unusually massive muscles of normal fibre length.

It seems reasonable to ask if mammals can attain muscle stresses, while running, as high as those attained during peak isometric contraction (0.3 MPa). Larger stresses than those attained during isometric contraction can be developed when a fully activated muscle is being forcibly stretched (Flintney and Hirst, 1978; Cavagna et al., 1981), doing negative work. When the foot first contacts the ground, while running, the active digital flexors and ankle extensors are elongated before subsequently shortening (Alexander and Vernon, 1975; Biewener et al., 1981; Goslow et al., 1981; and Alexander et al., 1982), and thus could conceivably attain stresses that meet or exceed levels reached at peak isometric contraction. Jayes and Alexander, (1982) calculated that while galloping, the distal limb muscles of greyhounds met and exceeded stresses of 0.3 MPa, confirming that these high stress values are realistically attainable during fast locomotion. However, what we do know

is that the stresses reached during isometric contraction for a variety of vertebrates is constant, and for this reason this value is used in determining the maximum force a muscle is capable of exerting, and consequently the potential maximum tendon stress.

5.2.3 Tendon Dimensions

The allometric analysis of tendon length and cross-sectional area, for non-hoppers, shows that tendons generally have dimensions predicted by geometric scaling (Figs. 4.7 -4.8; Table 4.3), i.e., $L_t \propto M_b^{0.33}$ and $A_t \propto M_b^{0.67}$. This is in accord with observations made by Alexander et al., (1981) and Peterson et al., (1984). The only exception being the total cross-sectional area of the common digital extensors, which exhibit negative allometry, meaning that they have thinner tendons than would be predicted by geometric scaling.

On the other hand, the tendons of the gastrocnemius and plantaris of the kangaroo rats and the plantaris of the wallaby are thicker than would have been predicted for non-hoppers of similar size. Biewener et al., (1981) state that the tendons of kangaroo rats are thicker than would be expected if they were geometrically similar to those of the wallaby, and for this reason they can not be stretched to the same degree as homologous tendons in the wallaby. However, what is interesting is that it is only the

gastrocnemius tendon of the wallaby that is as thin as predicted for non-hoppers of similar size.

5.3 Tendon Stress

Tendons are in series with muscles, therefore the maximum tension developed in a tendon cannot exceed the maximum tension (force) developed by its muscle. From equation 3.9 it follows that tendon stress is proportional to the ratio of the cross-sectional areas of the muscle fibres and tendon (A_m/A_t). Geometric scaling would predict the area ratio and thus the maximum stresses tendons experience to be independent of body mass (Appendix A). However, empirically this is not the case. Even though tendon cross-sectional area for digital flexors and ankle extensors scales geometrically, their muscle fibre cross-sectional areas do not, but instead scale with positive allometry. Therefore these muscles of larger mammals are able to exert greater forces than if they were geometrically similar to those of smaller mammals, and the equivalent tendons of larger mammals experience potentially greater stresses than do tendons of smaller mammals. The tendon stresses for the digital extensors also scale with positive allometry, but for different reasons. Even though muscle fibre cross-sectional area scales isometrically, the tendon cross-sectional area scales with negative allometry, resulting in the area ratio and, therefore, the maximum

stresses the tendons of the common digital extensor can experience, increasing with body mass. This does not, however, occur to the same degree as it does with the digital flexors.

Both the muscle fibre and the tendon cross-sectional areas are large for bipedal hoppers, but the ratio of the two dimensions falls within the range predicted by the allometric constants for non-hoppers. Of the bipedal hoppers, only the gastrocnemius tendon of the wallaby suffers high stresses (Table 5.2), due to the relative thinness of this tendon compared to the force that its muscle is capable of exerting.

The allometric constants of the muscle/tendon area ratio predict that the common digital extensor tendon, even in a 545 kg specimen, cannot be broken in tension in vivo because the stresses that the tendon experiences (Table 5.2) do not exceed its ultimate strength, since its muscle cannot exert anywhere near sufficient stress. This results in a factor of safety that is quite high (Table 5.3). Ker et al., (1988) proposed that this is the case for all tendons which experience low stresses, ($\sigma_t < 50$ MPa), and data from Tables 5.2 and 5.3 support this. Yet the allometric constants of the muscle/tendon area ratio predict that the highly stressed tendons of the plantaris, deep digital flexors and gastrocnemius of some of the larger mammals in this study are at risk. These tendons have high tendon stresses and safety factors that are two or less (Tables 5.2

and 5.3). If these allometric trends continued in very large animals (over 500 kg in body mass), a point would be reached at which the plantaris muscle was strong enough to break its own tendon. Alexander (1985) similarly noted this problem (based on the ankle extensor data of Alexander et al., 1981). Another factor that would lead to safety factors being reduced below those calculated in Table 5.3 would be if the muscles were loaded while they were forcibly stretched, resulting in muscle stresses larger than 0.3 MPa (Flitney and Hirst, 1978; Cavagna et al., 1981; Biewener et al., 1988; Ker et al., 1988). This could conceivably occur when an animal is landing from a fall (Alexander, 1981), or when it is startled (Biewener et al., 1988).

Why then, is it not common that the tendons of the digital flexors and ankle extensors in larger mammals rupture during locomotion? There are four possible reasons for this. 1) Perhaps the estimated maximum muscle stress of 0.3 MPa for an isometric contraction is too high. Biewener et al., (1988) and Perry et al., (1988) suggest a value of 0.2 MPa, which would effectively decrease the maximum tendon stress values in Table 5.2 by 33%. This however, would still not be enough to remove the plantaris tendon of the larger mammals from risk. 2) Perhaps the maximum tendon strength is greater than 100 MPa. Bennett et al., (1986) suggest that if tendon stress concentrations at clamps during tensile testing could be eliminated, higher values of tendon strength would become evident. However, even if

Table 5.2. Estimated maximum in vivo stresses (σ_t) in mammalian limb tendons, based on area ratios (A_m/A_t) in Figure 4.9 and assuming the maximum muscle stress is 0.3 MPa. The symbol, -, indicates that no stress value was calculated due to absence of muscle tissue or literature values.

Maximum tendon stress in MPa				
Mammal	PLA	DDF	GAS	CDE
Camel (545kg)	-	56	26	34
Cow (454kg)	84	66	30	23
*Camel (402kg)	-	26	31	-
Grizzly bear (338kg)	77	29	21	13
Persian onager (224kg)	101	82	34	54
Elk (160-205kg)	92-96	32-35	33-63	13-21
Bearded gnu (205kg)	173	71	85	30
Lion (200kg)	47	28	43	10
Horned oryx (110kg)	93	34	36	20
White-tail deer (28-98kg)	52-101	36-52	58-71	12-22
Mule deer (97kg)	102	51	61	29
Dog (28-36kg)	89-107	27-38	59-75	17-27
Snow leopard (34kg)	43	24	42	9
Russian saiga (29kg)	101	53	67	28
Springbok (28kg)	97	32	80	27
Antelope (20kg)	64	28	30	17
Muntjac (11-13kg)	44-94	25-46	26-34	17-20
Indian hog deer (13kg)	46	14	32	12
*Wallaby (10kg)	61	-	85	-
Cat (5-7kg)	33-36	21-24	49-57	9-14
Jack-rabbit (2-3kg)	50-73	21-30	90-112	33-37
Muskrat (0.6kg)	41	18	39	10
Grey squirrel (0.6kg)	28	18	32	12
Ferret (0.5kg)	20	11	16	4
Ground squirrel (0.5kg)	28	10	27	7
Guinea pig (0.4kg)	11	6	18	-
Wood rat (0.2kg)	7	10	10	11
*Kangaroo rat (0.1kg)	16-22	-	24-32	-
Gerbil (0.04kg)	18	6	15	9

* asterisk indicates tendon stresses based on literature values for A_m/A_t (see Materials and Methods).

Table 5.3. Estimated factors of safety in mammalian limb tendons, based on tendon stresses in Table 5.2 and assuming the ultimate tendon strength is 100 MPa. The symbol, -, indicates that no safety factor value was calculated.

Factors of safety				
Mammal	PLA	DDF	GAS	CDE
Camel (545kg)	-	1.8	3.8	2.9
Cow (454kg)	1.2	1.5	3.3	4.3
*Camel (402kg)	-	3.8	3.2	-
Grizzly bear (338kg)	1.3	3.4	4.8	7.7
Persian onager (224kg)	1	1.2	2.9	1.8
Elk (160-205kg)	1	3.1-2.8	3-1.6	7.7-4.8
Bearded gnu (205kg)	0.6	1.4	1.2	3.3
Lion (200kg)	2.1	3.6	2.3	10
Horned oryx (110kg)	1.1	3	2.8	5
White-tail deer (28-98kg)	2-1	2.8-1.9	1.7-1.4	8.3-4.5
Mule deer (97kg)	1	2	1.6	3.4
Dog (28-36kg)	1	3.7-2.6	1.7-1.3	5.9-3.7
Snow leopard (34kg)	2.3	4.2	2.4	11
Russian saiga (29kg)	1	1.9	1.5	3.6
Springbok (28kg)	1	3.1	1.25	3.7
Antelope (20kg)	1.6	3.6	3.3	5.9
Muntjac (11-13kg)	2.3-1.1	4-2.2	3.8-2.9	5.9-5
Indian hog deer (13kg)	2.2	7.1	3.1	8.3
*Wallaby (10kg)	1.6	-	1.2	-
Cat (5-7kg)	3	4.8-4.2	2-1.75	11-7.1
Jack-rabbit (2-3kg)	2-1.4	4.8-3.3	1.1-0.9	3-2.7
Muskrat (0.6kg)	2.4	5.6	2.6	10
Grey squirrel (0.6kg)	3.6	5.6	3.1	8.3
Ferret (0.5kg)	5	9	6.25	25
Ground squirrel (0.5kg)	3.6	10	3.7	14.2
Guinea pig (0.4kg)	9.1	16.7	5.6	-
Wood rat (0.2kg)	14.3	10	10	9
*Kangaroo rat (0.1kg)	6.3-4.5	-	4.2-3.1	-
Gerbil (0.04kg)	5.5	16.7	6.7	11

* asterisk indicates tendon stresses based on literature values for A_m/A_t (see Materials and Methods).

ultimate tendon strength was as high as 150 GPa, the plantaris tendon of a few of the larger ungulates would still be at risk (safety factor of two or less). 3) This suggests that the allometric relationships for tendon stress, described in this study, reach a size limit. Mammals of the largest sizes would have to scale with a decreased value for the scaling exponent of the area ratio (differential allometry) or else the plantaris tendons would break in tension. Close examination of Figure 4.9 reveals that for the very largest mammals (>200kg) the values for the area ratio of the plantaris and gastrocnemius fall below their respective regression lines, ie., maximum tendon stresses for these mammals are lower than would be predicted by extrapolation from smaller mammals. Similarly, the plantaris area ratio value for the buffalo and elephant in Alexander et al's., (1981 [see Fig 4]) study falls below its regression line. This indicates a possible trend toward reduced allometric exponents for tendon stress in the largest mammals. 4) A limb posture-based mechanism may be responsible for reducing ankle extensor and digital flexor tendon stresses in large mammals. Biewener (1989) noted that both muscle and bone have similar peak functional stresses, ensuring a uniform safety factor (2 - 4) in mammalian species. In other words, peak functional stresses for both muscle and bone are independent of body mass. Yet on the basis of the scaling of limb bone dimensions, peak skeletal stress is predicted to increase as $M_b^{0.28}$

(Biewener, 1982). How did he explain this discrepancy? It appears that similar peak bone stresses and muscle stresses in large and small mammals are achieved primarily by a size-dependent change in locomotor limb posture: small animals run with crouched postures, whereas larger species run more upright (Figure 5.1). By adopting an upright posture, large mammals align their limb segments more closely with the ground reaction force (F_g). This reduces the moment arm of the ground reaction force (R), and as a result the "effective mechanical advantage" ($EMA = r/R$) of the ankle extensors is increased, substantially reducing the forces that their muscles must exert (F_m) to support the animal while running (Biewener, 1989, 1990). As the force exerted by muscles constitutes the major fraction of force that must be resisted by limb bones during locomotion, the observed increase in muscle mechanical advantage accounts for 85% of the decrease in force required to maintain similar skeletal stresses in large and small animals (Biewener, 1989, 1990). As tendons are attached in series with their muscles, this functional decrease in muscle force would consequently cause the tendon stresses to be lower than those that would occur if the posture was unaltered in larger mammals. During locomotion, the tendons of the largest mammals generally do not experience dangerously high stresses (Table 5.1), allowing for more uniform factors of safety over a large body size range.

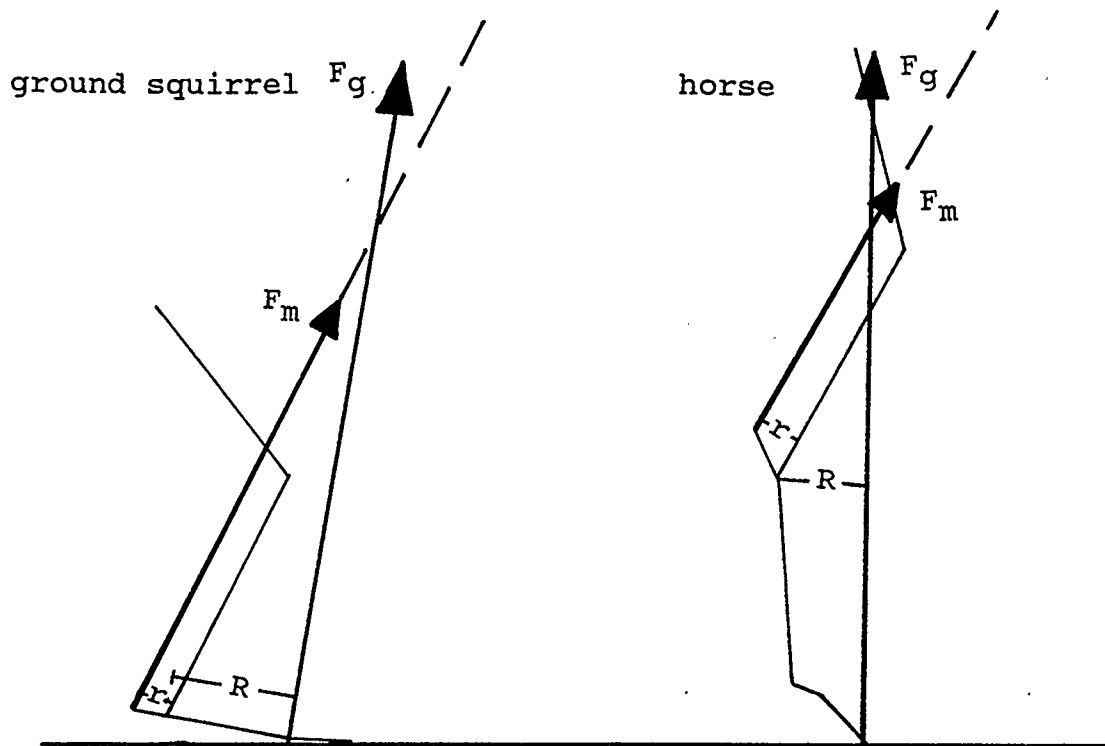


Figure 5.1. A schematic representation of the hindlimb of a ground squirrel (0.14kg) which adopts a crouched posture versus a horse (280kg) (drawn to equivalent scale) which is more upright, at corresponding stages of their strides. F_g is the ground reaction force, R is the moment arm of the ground reaction force, F_m is the force exerted by the plantaris and gastrocnemius muscles, and r is the moment arm of these muscles. The effective mechanical advantage (EMA) for these muscles about the ankle joint is the ratio of r/R . The more crouched posture of the squirrel results in a greater value for R for its size, compared to the horse. The moment arm ratio about the ankle joint multiplied by the ground reaction force will give the muscle force as: $(R/r)F_g = F_m$. Thus a more upright posture aligns the limb closer to F_g , increasing the muscle's effective mechanical advantage as well as decreasing the force exerted by the muscles. F_m is a much smaller multiple of F_g for the horse than the squirrel. Note the magnitudes of F_m are not drawn to scale (adapted from Alexander, 1988 and Biewener, 1983 & 1990).

Biewener's (1989) limb posture and muscle mechanical advantage explanation for stress similarity only covers animals for which body masses range from 0.1 to 300 kg. Mammals that are much greater in body mass also have much more robust skeletons, where bone length scales to bone diameter^{0.5}. Further adjustments in the alignment of limb posture may have limited utility and bone diameter has to increase to maintain stresses within an acceptable limit (Bertram and Biewener, 1990; Biewener, 1990). Economos (1983) showed that allometric equations relating body length to body mass for medium to large mammals (>20 kg) had smaller exponents ($b=0.27$) than for smaller mammals (< 20 kg) ($b=0.34$). Above 20 kg, body length could not increase as fast as geometric similarity requires, or bending stress would be unsupportable. These again are examples of differential allometry; once an animal reaches a certain extreme body size, the rules for stress reduction change, as suggested above for tendon stresses (explanation #3).

5.4 Length Factor

The fibres of some muscles are too short to allow the muscle to stretch its tendon fully. The muscle cannot provide the tendon's strain energy at high loads, let alone supply energy to the external system (Ker et al., 1988). The muscles of ungulates typically have extremely short fibres (Figure 4.5). The maximum tendon stress for the

plantaris tendon of a 98 kg white-tailed deer, for example (Table 5.2), is 101 MPa. From Figure 4.1, the corresponding strain is about 9.7%. The plantaris has fibre lengths of about 9.8 mm, and the length of the tendon is about 572 mm. Assuming tendon strain is the same throughout its length, the maximum extension of the tendon would be about 55.5 mm. The fractional range over which sarcomeres operate is 0.25 (Ker et al., 1988), thus the plantaris muscle would only contract through about 2.5 mm, and thus be unable to stretch its tendon more than 0.5%. Therefore, most of the tendon's strain energy must come from the external system when the muscle-tendon unit is first loaded (stretched) as the foot contacts the ground. On the other hand, the muscle fibres of the common digital flexors for the same specimen (98 kg) are much longer, having lengths of approximately 38 mm and a tendon length of 482 mm. The maximum tendon stress is 22 MPa with a corresponding strain of 3%, and maximum extension of 14.5 mm. The muscle of the common digital extensor would contract through 9.5 mm, taking up a large portion of the possible tendon extension.

The dimensionless fibre length factor (L), defined as the ratio of the muscle fibre length to the extension of its tendon when the muscle is producing maximal force (0.3 MPa), is used to describe the relative importance of the muscle versus tendon length changes in determining displacement at the joint at full load, and therefore strain energy storage capabilities at maximal loads (Ker et al., 1988; Shadwick,

1990). According to Ker et al's., (1988) theory for the optimization of tendon thickness, the muscle is less important than the tendon in joint displacement when $L < 4$, and even more so when $L < 2$. In these situations the dimensions of the muscle-tendon unit have been optimized for effective elastic energy storage. This is characteristic of tendons that are relatively long and thin, and whose corresponding short-fibred muscles can impose high stresses (such as the plantaris). Such tendons are ideally suited to act as locomotory springs (Alexander, 1984). When a tendon acts as a spring the only necessary role for the muscle is to maintain tension. Short fibres are mechanically adequate to maintain this tension and bring the benefit of small mass (Ker et al., 1988), which is critical for larger cursors that typically have reduced muscle mass in the distal region of their limbs.

Ker et al's., (1988) theory also states that the dimensions of the muscle-tendon unit have been designed for control of joint displacement and minimal total mass when $L > 4$. Figure 4.10 shows that for nearly all body sizes in this study the plantaris tendon, having values of L less than 4, is designed for elastic strain energy storage. As body size increases this capacity is substantially amplified, especially in the ungulates that have very short plantaris muscle fibres and long tendons. The muscle-tendon units of the deep digital flexors, gastrocnemius and to some degree the plantaris, from mammals with a body mass of

about 1 kg or less (specimens that generally exhibit an ambulatory style locomotion) are generally designed for joint displacement. While those specimens with a body mass above 1 kg (cursors) generally have these same muscle-tendon units designed for elastic strain energy storage (Figure 4.10).

The length factor of the digital extensors for all the less specialized cursorial and ambulatory mammals is generally greater than 4. This trend indicates that the muscle-tendon unit of the digital extensors for these specimens is designed primarily for the displacement of the metatarsal-phalangeal joint (Figure 4.10). In contrast, the muscle-tendon unit of the common digital extensor for ungulates and hares (highly specialized cursors) does not appear to be designed for joint displacement, having values of $L < 3$ and more commonly $L < 2$ over their entire size range (Figure 4.10). Ker et al., (1988) also found that the digital extensor of the horse (a large ungulate) does not have the high length factor typically associated with this tendon. However, it cannot be said that digital extensors act as springs as described by Alexander (1984) because they are not under load when the foot is on the ground. Ker et al., (1988) suggested that either the thinness of these tendons may simply reflect the great emphasis in design these highly specialized cursors place in minimizing mass in the distal parts of the limb, or they do somehow act as biological springs by a mechanism yet to be described.

Furthermore, Ker et al., (1988) proposed that tendons that are designed to store elastic strain energy and function as springs during locomotion should have the following features: attachment to muscles with relatively short fibres, $A_m/A_t > 75$, maximum in vivo $\sigma_t > 25$ MPa and $L < 2$. Figures 4.5, 4.9 and 4.10 and Table 5.2 indicate that the digital flexors and ankle extensor of mammals greater than 1kg in body mass generally fall into this category, whereas the digital extensors do not. The digital extensors in this study (with exception of those of some of the ungulates and the hares) generally have relatively long muscle fibres, $A_m/A_t < 50$ MPa, maximum in vivo $\sigma_t < 15$ MPa, and $L > 4$. According to Ker et al. (1988), digital extensor tendons, and others not involved in elastic energy storage (such as the digital flexors and ankle extensors of mammals less than 1 kg in body mass), are optimized in thickness to provide a relatively inextensible link between muscle and bone, while at the same time minimizing the combined muscle-tendon mass. These tendons (digital extensors and all tendons from animals less than 1 kg in body mass) have high safety factors (Table 5.3), and are relatively thick for the force-generating capabilities of their muscles, and consequently will not be stretched enough to store large quantities of strain energy. The digital flexors and ankle extensor tendons of mammals greater than 1 kg in body size, on the other hand, have low safety factors (Table 5.3) and relatively slender tendons when viewed in the light of the

force-generating capabilities of their muscles. Consequently these tendons will be stretched sufficiently to store large quantities of elastic strain energy.

Biewener and Bertram (1991) show this trend also exists for bipedal hoppers. A trade-off exists in the design of the ankle extensor tendon for effective elastic energy storage in the large red kangaroo (relatively thin tendon) versus acceleration and effective motor control in the much smaller kangaroo rat (relatively thick tendon).

5.5 Capacity for Storage of Elastic Strain Energy

The scaling exponents of the maximum capacity for elastic strain energy storage for all the tendons examined in this study is greater than one (Table 4.4 and Figure 4.11). This indicates that larger mammals have a greater capacity for storage of elastic strain energy than do smaller ones. This is especially evident in the digital flexors and ankle extensor tendons, which experience high stresses and therefore high strains. For example, the maximum stress of the plantaris tendon of a 454 kg cow is about 84 MPa (Table 5.2). From Figure 4.1 the corresponding maximum strain is approximately 8.6%. Tendon volume, calculated as length (L_t) by cross-sectional area (A_t), is about 88254 mm³. From equation 3.11 the plantaris tendon of a 454 kg cow can store up to 320 Joules of elastic strain energy. The average hysteresis, a measure of the amount of

input energy lost per tendon extension, as calculated in this study is 9.3%. As tendon material properties are independent of body mass (Table 4.1), the amount of elastic strain energy released from the plantaris tendon in recoil is about 290 Joules in each stride.

Conversely the homologous tendon from a much smaller mammal, such as a 0.47 kg ground squirrel, will not experience as much stress, because its muscle, due to its relatively diminutive size compared to its tendon, can not exert forces large enough to stretch the tendon a great deal. This is similar to observations made by Biewener et al., (1981), concerning tendon strain in an equally small mammal, the kangaroo rat. Maximum plantaris tendon stress in the ground squirrel is about 28 MPa (Table 5.2) and the corresponding maximum strain is 4.5% (Figure 4.1). Tendon volume is about 32 mm^3 . From equation 3.11 the maximum elastic strain energy that the plantaris tendon of a 0.47 kg ground squirrel can store is 0.02 Joules. Normalized for body mass (on a mass-specific basis), a ground squirrel can only store 0.04 J/kg of elastic strain energy in its plantaris tendon, whereas a cow (1000 fold larger) can store up to 0.70 J/kg in the same tendon. Clearly, large mammals have a greater capacity, per unit of animal mass, to store elastic strain energy in their tendons (especially in the highly stressed digital flexors and ankle extensors) than do smaller mammals. However, there does not appear to be a difference between the capacity of large and small mammals

to store elastic strain energy in the digital extensor tendons, as the scaling exponent for these tendons is not significantly different from one. This is to be expected since the digital extensor muscle-tendon unit is not loaded (and consequently strained) when the foot is on the ground. Rather, any elastic strain energy stored in these tendons is due solely to the muscle's ability to stretch the tendon (via muscle contraction) during the swing phase of a stride.

5.6 Elastic Strain Energy as an Energy Saving Mechanism

Highly stressed tendons, such as those of the digital flexors and ankle extensors of large mammals, potentially have an important energy saving role in locomotion. They are stretched in each step as the foot impacts the ground, briefly storing elastic strain energy. This will be released again as the tendons subsequently recoil elastically before the foot leaves the ground. These tendons of the distal limb act as passive biological springs (Alexander, 1984), and result in the expenditure of smaller amounts of metabolic energy than would otherwise be necessary if the muscles alone were responsible for supplying all the energy for the positive and negative work of each stride. For the cow, the negative work required of the muscles in each stride is reduced by up to 0.7 J/kg and the positive work by $0.7(R_t)$ J/kg (where R_t is the resilience of the tendon [Alexander, 1980]).

These values, of course, represent the maximum amounts of strain energy that can be stored and released. To illustrate the substantial energy saving capabilities of storage and release of elastic strain energy in large mammals, such as the cow, it is necessary to know the amount of energy each limb typically expends per stride during fast locomotion. The present study, however, did not include an investigation of the energetics of fast locomotion, nor are there any data for the actual muscle and tendon stresses the cow experiences during fast locomotion, but only estimations of the maximum possible stresses. Estimations of the stresses in these elements, however, can be determined if we know the forces exerted by the feet on the ground (as in Figure 5.1) while a specimen is running. Alexander et al., (1979) estimated the forces on the hind and forelimbs of an African buffalo (500kg), based on analysis of films of an individual running at full speed. Assuming the duty factors for a 454 kg cow running similarly are the same as those for the buffalo in Alexander et al.'s., (1979) study, and following the methods outlined by those authors, the estimated force at the midpoint of the period of contact of each hindlimb with the ground (F_g) is about 4000 N. The gastrocnemius and plantaris tendon and muscle dimensions for the buffalo (Alexander et al., 1979) are very similar to those observed for the 454 kg cow in this study. Assuming the plantaris and gastrocnemius muscles of the cow have a similar moment arm (r) of 0.085 m about the ankle joint, and

a moment arm of the ground reaction force (R) of 0.22 m, then the force exerted together by the plantaris and gastrocnemius (as in Figure 5.1. $F_m = F_g R/r$) is about 10,500 N. The stress in these muscles would be about 0.18 MPa (somewhat lower than that expected from a maximum isometric contraction). The fibre areas for the plantaris and gastrocnemius muscles in the cow are 26400 and 30700 mm², respectively. If the same stress acted in both muscles, the plantaris would contribute 4860 N and the gastrocnemius 5640 N. The cross-sectional area of the plantaris tendon is 95 mm², so tendon stress would be about 51 MPa. Similarly, tendon area for the gastrocnemius is about 5640 mm², so tendon stress would be 18 MPa. Note that the stresses that would be incurred in the cow while running, would be lower than the calculated maximum tendon stresses in Table 5.2. Based on equation 3.11 and Figure 4.1 the plantaris and gastrocnemius tendons would store, respectively, about 140 and 37 Joules of elastic strain energy per stride. Note that these values are lower than those predicted to be the maximum storage capacity, since the calculated tendon stresses of the running individual are lower than the maximum stresses possible.

Following a method used by Dimery et al., (1986), the amount of positive and negative work each hindlimb of the cow would do in each stride is calculated as follows. Running mammals lose and regain kinetic and gravitational potential energy, amounting on average to 0.7 J/kg of body

mass, for every meter travelled (Heglund et al., 1982). The forelegs of most quadrupedal mammals each support about 30% of body weight and the hind legs each support 20%, while the animal is moving (Jayes & Alexander, 1978; Alexander & Jayes, 1983). The work done by the legs is presumably divided between them in approximately the same proportion, thus, each hindlimb does about 0.14 J/kg of negative and positive work, for each meter travelled. In a separate study Alexander, et al., (1977) calculated stride lengths of 3.5 meters for the African buffalo (500 kg) running at full speed (7 m/s). Assuming similar stride lengths for the cow, in such a stride each hind limb would do about 0.14 J/kg m x 454 kg x 3.5 m = 222 J of negative and positive work. The total strain energies for the plantaris and gastrocnemius alone (140 and 37 J) represent large fractions of this work. Presumably the tendons of the deep digital flexors would also contribute to energy savings. Thus most of the negative and positive work can apparently be performed passively by these tendons in large mammals leaving only a minor part to be performed by the muscle at metabolic cost (Alexander, 1974; Alexander and Vernon, 1975; Alexander et al., 1982; Dimery and Alexander, 1985; Dimery et al., 1986). Large mammals which are capable of storing large quantities of elastic strain energy, such as the cow in this study, will therefore use considerably less metabolic energy in each stride, resulting in lower transport costs per kilogram of body mass.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Two new major findings have resulted from the tensile tests carried out in this study.

- 1) The tendons of the digital flexors and ankle extensors (those most likely to act as springs during locomotion), have the same material properties (i.e., elastic modulus and hysteresis), as the tendons of the digital extensors (those not likely to function as springs during locomotion).
- 2) The material properties of these functionally different tendons are both species and body mass independent ($\propto M_b^{0.00-0.03}$).

The morphometrics portion of this study also revealed some interesting findings regarding the mechanical potential of both muscle and tendon in determining the capacity for storage of elastic strain energy with increasing body size

- 3) The muscle fibre cross-sectional area, an approximation of muscle force, of the digital flexors and ankle extensors scales with positive allometry ($\propto M_b^{0.77-0.91}$), but scales isometrically ($\propto M_b^{0.69}$) in the digital extensors.
- 4) The cross-sectional area of the spring-like tendons scales isometrically ($\propto M_b^{0.64-0.68}$), while the digital extensor tendon area scales with negative allometry ($\propto M_b^{0.56}$). The tendon length for all tendon types scales isometrically ($\propto M_b^{0.34-0.38}$).

- 5) Therefore the muscle/tendon area ratio scales with positive allometry in all cases ($\propto M_b^{0.08-0.24}$). Assuming the maximum isometric stress developed by a muscle is constant, then this ratio is proportional to the maximum stress the muscle can exert on its tendon.
- 6) The dimensionless length factor suggests that the muscle-tendon unit of the digital flexors and ankle extensors in larger cursorial mammals is designed for elastic energy storage ($L < 2$), while in smaller ambulatory mammals these muscle-tendon units (excluding the plantaris) may play a greater role in joint displacement. The digital extensors in the more generalized quadrupedal mammals, not being highly stressed, are designed for joint displacement.
- 7) The maximum amount of elastic strain energy stored in the tendons is proportional to stress x strain x volume. The capacity for storage of elastic strain energy scales with positive allometry for tendons of the digital flexors and the ankle extensors ($\propto M_b^{1.14-1.38}$), but scales almost isometrically for the tendons of the digital extensors ($\propto M_b^{1.08}$). Thus the highly stressed, spring-like tendons, are capable of storing more elastic strain energy in larger mammals than in smaller ones. While the potential for storage of elastic strain energy in the tendons of the digital extensors keeps in proportion to increases in body mass.

The results of this study demonstrate that the plantaris, deep digital flexors and gastrocnemius are

designed to play a potentially more important role in elastic energy storage with increasing body size, while the digital extensors, which do not act as springs anyway, are not. This is not because of any difference in material properties of the tendons (as suggested by Woo, 1982 and Shadwick, 1990), or disproportionate scaling in their dimensions with size (as suggested by Biewener et al., 1981). Rather, it is because of muscle force capability increasing with positive allometry, i.e., these muscles in larger mammals are capable of exerting greater stresses on their tendons than they are in smaller mammals.

It has been shown that storage and release of elastic strain energy can act as an energy saving mechanism during fast locomotion. As the highly stressed digital flexors and ankle extensors have the potential to store large amounts of strain energy as body size increases, it follows that the role of these tendons in energy savings also increases with body size. This results in lower transportation costs per kilogram of body mass for larger mammals.

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APPENDIX A

Allometric relationships predicted by geometric scaling	Allometric relationships based on empirical data for each muscle and/or tendon unit			
	PLA	DDF	GAS	CDE

Volume and mass can be equated as equal as most animals have a density of one, therefore geometric scaling would predict that muscle mass would scale to body mass with an exponent of one. Empirical data for muscle mass scales geometrically.

$$M_m \propto M_b^{1.00} \quad \propto M_b^{0.97} \quad \propto M_b^{1.03} \quad \propto M_b^{0.97} \quad \propto M_b^{0.93}$$

Geometric scaling predicts all lengths to scale to the one third power of body mass, however the empirical data for muscle fibre length scales with negative allometry in each case.

$$L_m \propto M_b^{0.33} \quad \propto M_b^{0.05} \quad \propto M_b^{0.18} \quad \propto M_b^{0.21} \quad \propto M_b^{0.24}$$

$$A_m = M_m / L_m \cdot \rho_m$$

Geometric scaling predicts all areas to scale to the two thirds power of body mass, however the empirical data for muscle fibre cross-sectional area (with the exception of the digital extensors) scales with positive allometry.

$$A_m \propto M_b^{0.67} \quad \propto M_b^{0.91} \quad \propto M_b^{0.85} \quad \propto M_b^{0.77} \quad \propto M_b^{0.69}$$

Tendon length scales geometrically

$$L_t \propto M_b^{0.33} \quad \propto M_b^{0.35} \quad \propto M_b^{0.38} \quad \propto M_b^{0.34} \quad \propto M_b^{0.35}$$

Tendon cross-sectional area scales geometrically, with the exception of the digital extensors which scales with negative allometry.

$$A_t \propto M_b^{0.67} \quad \propto M_b^{0.68} \quad \propto M_b^{0.64} \quad \propto M_b^{0.68} \quad \propto M_b^{0.56}$$

$$A_m/A_t \propto \sigma_t$$

Geometric scaling predicts that tendon stress is independent of body mass, however the empirical data for all tendons shows that **tendon stress** scales with positive allometry.

$$\sigma_t \propto M_b^{0.00} \quad \propto M_b^{0.24} \quad \propto M_b^{0.21} \quad \propto M_b^{0.08} \quad \propto M_b^{0.13}$$

$$U = (1/2 \sigma_t \cdot \epsilon_t) (L_t \cdot A_t)$$

Based on anatomical data alone and assuming a linear stress-strain curve with elastic modulus independent of body mass, geometric scaling would predict that the maximum capacity for storage of elastic strain energy would scale with an exponent of one (proportional to tendon volume). However the empirical data shows that the **maximum capacity for storage of elastic strain energy** scales with positive allometry, as neither stress nor strain scale independent of body mass.

$$U \propto M_b^{1.00} \quad \propto M_b^{1.38} \quad \propto M_b^{1.32} \quad \propto M_b^{1.13} \quad \propto M_b^{1.08}$$