Scaling of elastic energy storage in mammalian limb tendons: do small mammals really lose out?

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It is widely believed that elastic energy storage is more important in the locomotion of larger mammals. This is based on: (a) comparison of kangaroos with the smaller kangaroo rat; and (b) calculations that predict that the capacity for elastic energy storage relative to body mass increases with size. Here we argue that: (i) data from kangaroos and kangaroo rats cannot be generalized to other mammals; (ii) the elastic energy storage capacity relative to body mass is not indicative of the importance of elastic energy to an animal; and (iii) the contribution of elastic energy to the mechanical work of locomotion will not increase as rapidly with size as the mass-specific energy storage capacity, because larger mammals must do relatively more mechanical work per stride. We predict how the ratio of elastic energy storage to mechanical work will change with size in quadrupedal mammals by combining empirical scaling relationships from the literature. The results suggest that the percentage contribution of elastic energy to the mechanical work of locomotion decreases with size, so that elastic energy is more important in the locomotion of smaller mammals. This now needs to be tested experimentally.

Keywords: strain energy; locomotion; muscle energetics

1. INTRODUCTION

During locomotion, an animal must do mechanical work to swing its legs, to lift its body against gravity and to maintain its forward speed. This work is done partly by active muscle contraction and partly by tendons, which act like springs, storing elastic energy when they are stretched and then releasing this energy to do work later in the stride. This spring-like action of tendons is thought to benefit the animal by reducing the metabolic energy required for locomotion, so increasing efficiency (Alexander 1984). Energy savings due to elastic energy storage are widely believed to be more important in the locomotion of large mammals

than they are in smaller species. Here we argue that the available evidence does not support this view.

The idea that elastic energy storage is more important in larger mammals is based predominantly on two pieces of evidence. Firstly, it has been shown that stored elastic energy does a greater proportion of the mechanical work of locomotion in kangaroos than it does in the smaller kangaroo rat (Biewener *et al.* 1981). However, kangaroos scale very differently from quadrupedal mammals (Bennett 2000), and kangaroo rats have disproportionately thick tendons which are necessary to withstand the high forces involved in jumping, but which prevent significant elastic energy storage during normal hopping (Biewener & Blickhan 1988). Therefore this comparison cannot be generalized to other mammals.

Secondly, it has been calculated from measurements of muscle and tendon dimensions that the capacity for elastic energy storage per kilogram of body mass increases with size in both kangaroos (Bennett & Taylor 1995) and quadrupedal mammals (Alexander *et al.* 1981; Pollock & Shadwick 1994*a*). However, although this provides an important insight into the effects of size on the maximum energy storage capacity, it does not necessarily indicate how the functional importance of elastic energy storage changes with size. The efficiency of locomotion is influenced not by the elastic energy storage relative to body mass, but by the elastic energy storage relative to the mechanical work of locomotion, and it is this latter measure which is usually used to assess the importance of elastic energy to an animal (e.g. Biewener *et al.* 1981; Alexander *et al.* 1982; Ker *et al.* 1987).

The extent to which elastic energy contributes to the mechanical work of locomotion will not scale in the same way with size as the maximum energy storage capacity. The reason for this is that the mechanical work of locomotion per kilogram of body mass is directly proportional to the distance travelled (Blickhan & Full 1993), so that larger animals, with their longer strides, must do relatively more work per stride. Because each tendon can store and return elastic energy only once per stride, this greater mechanical work will tend to offset the greater elastic energy storage capacity of larger mammals. Therefore, the contribution of elastic energy to the mechanical work of locomotion cannot increase with size as rapidly as the energy stored per stride, and could be greater in smaller mammals.

Here we consider how the functional importance of elastic energy storage in locomotion is related to size in quadrupedal mammals. Because the maximum elastic energy storage capacity is likely to be utilized only rarely, we instead consider elastic energy storage in animals moving at submaximal speeds. Because the speed at which an animal prefers to move depends upon its size, we compare animals moving at equivalent speeds, rather than at the same speed. We derive expressions for the scaling of elastic energy storage, and the scaling of the mechanical work of locomotion, using empirical relationships from the literature. We combine these expressions to predict how the ratio of elastic energy storage to mechanical work changes with size in quadrupedal

mammals moving at equivalent speeds. Our aim is to predict whether the increase in stride length with size is sufficient to offset the greater energy storage capacity of large mammals to the extent that elastic energy is more important in the locomotion of smaller mammals.

2. DERIVATION

In order to be able to predict elastic energy storage in a tendon, it is necessary to know the force to which it will be subjected. Previously, the capacity for energy storage has been predicted by assuming that the maximum force on a tendon is proportional to the maximum isometric force that its muscle can generate, which can be estimated from muscle cross-sectional area (Pollock & Shadwick 1994a; Bennett & Taylor 1995). However, this method cannot be used here without assuming that the muscle forces generated by animals of different sizes moving at equivalent speeds are a fixed proportion of the maximum isometric force. Here we take an alternative approach by estimating tendon forces from the 'effective mechanical advantage' (EMA) of the limb. This is the ratio of the extensor muscle moment arm to the ground reaction force (GRF) moment arm about the limb joints and is approximately equal to the ratio of peak GRF to peak muscle force (Biewener 1989). Therefore, if EMA and peak GRF are known, muscle and tendon forces can be predicted.

Biewener (1989) showed that the mean value of EMA increases with body mass (m) in quadrupedal mammals, in proportion to $m^{0.26}$. This relationship was determined at the trot–gallop transition speed, which has been shown to be an equivalent speed for mammals of different sizes (Heglund *et al.* 1974). However, EMA did not change significantly with speed or gait (Biewener 1989), so this scaling exponent also applies at other equivalent speeds. We will assume that peak GRF in quadrupedal mammals moving at equivalent speeds is proportional to body mass. This is supported by the results of Farley *et al.* (1993). It is also supported by the finding that duty factor is independent of size in quadrupedal mammals moving at equivalent speeds (Alexander & Jayes 1983; Biewener 1983), because animals moving with equal duty factor must have peak GRFs that are approximately proportional to body mass (Alexander *et al.* 1979). If EMA is proportional to $m^{0.26}$ and peak GRF is proportional to m, then peak tendon forces will be proportional to $m^{0.74}$ (Biewener 1989). This is similar to the value that would be predicted from limb muscle cross-sectional areas, which scale in proportion to approximately $m^{0.8}$ in mammals that do not hop (Alexander *et al.* 1981). In kangaroos, however, limb muscle cross-sectional areas are proportional to between $m^{0.81}$ and $m^{1.19}$, and EMA is independent of body mass (Bennett & Taylor 1995), so tendon forces and elastic energy storage would both be expected to increase much more rapidly with size than in quadrupeds.

To obtain an expression for the scaling of elastic energy storage per stride, we will assume that tendon elastic modulus is independent of animal size and that tendons scale isometrically, so that tendon lengths are

proportional to $m^{0.33}$ and tendon cross-sectional areas are proportional to $m^{0.67}$. Both these assumptions are supported by the findings of Pollock & Shadwick (1994a,b). Tendon stress is force divided by cross-sectional area, so forces proportional to $m^{0.74}$ will induce stresses proportional to $m^{0.07}$. The elastic energy stored per unit volume of tendon is given by the area under the tendon stress–strain curve. If the stress–strain relationship is approximated as linear, then stresses proportional to $m^{0.07}$ will induce strains proportional to $m^{0.07}$, so that the area under the curve is proportional to $m^{0.14}$. For isometrically scaling tendons, tendon volume will be proportional to body mass, so that the elastic energy stored per stride is proportional to the product of body mass and the energy stored per unit volume of tendon, as follows:

$$\text{elastic energy storage per stride} \propto m \times m^{0.14} = m^{1.14}. \tag{2.1}$$

The mechanical work that an animal does on its centre of mass when it moves one metre is proportional to its body mass (Blickhan & Full 1993). Stride length in mammals moving at equivalent speeds is approximately proportional to leg length, or to $m^{0.33}$ (Alexander & Jayes 1983; Heglund & Taylor 1988). Therefore, the work per stride, which is the product of work per metre and stride length, will scale as follows:

$$\text{mechanical work per stride} \propto m \times m^{0.33} = m^{1.33}. \tag{2.2}$$

The ratio of elastic energy storage to mechanical work can then be predicted by dividing equation (2.1) by equation (2.2) to give:

$$\frac{\text{elastic energy storage}}{\text{mechanical work}} \propto m^{1.14}/m^{1.33} = m^{-0.19}. \tag{2.3}$$

The negative scaling exponent for this ratio implies that the percentage contribution of elastic energy to the mechanical work of locomotion decreases with size in quadrupedal mammals. This suggests that elastic energy storage may play a greater role in the locomotion of small mammals than it does in larger species.

3. DISCUSSION

Therefore, on the basis of the above argument, we recommend an alternative interpretation of the evidence available in the literature. Pollock & Shadwick (1994a) have demonstrated that the elastic energy storage capacity relative to body mass will increase with size in quadrupedal mammals. In equation (2.1) we make a similar prediction for the elastic energy which is stored at each stride in quadrupedal mammals moving at equivalent speeds. However, equation (2.2) predicts that the mechanical work per stride will increase to a greater extent with size than the elastic energy stored per stride. This suggests that the contribution of elastic energy to the mechanical work of locomotion decreases with size in quadrupedal mammals, so that elastic energy storage is more important in the locomotion of smaller mammals.

An alternative approach to the question considered here would have been to assume that, in mammals

moving at equivalent speeds, the elastic energy stored per stride scales in the same way as the maximum capacity for elastic energy storage. The mean value of the scaling exponents calculated by Pollock & Shadwick (1994a) for the elastic energy storage capacity of mammalian limb tendons is 1.28. Using this instead of the exponent in equation (2.1) would give a ratio of elastic energy storage to mechanical work proportional to $m^{-0.05}$. This is closer to zero than the exponent in equation (2.3), suggesting the possibility that elastic energy storage is equally import-ant in large and small quadrupedal mammals. How-ever, it again does not support the view that elastic energy storage is more important in larger mammals.

Taylor (1994) also argued that elastic energy storage might be important in small, as well as large, animals. However, his argument relied on the assumption that the success of the spring-mass model in representing locomotion is an indication of the importance of elastic energy storage. This is not necessarily the case, because spring-like behaviour could be generated purely by active muscle contraction (Blickhan 1989). Here we have been able to predict the importance of elastic energy storage in animals of different sizes without making this assumption.

Further experimental evidence is needed to deter-mine the exact relationship between size and the importance of elastic energy storage. Mechanical work and elastic energy storage need to be measured in mammals of a wide range of sizes moving at an equivalent speed, such as the preferred trotting speed, using standardized protocols. There are several reasons why this is necessary. Firstly, systematic changes in locomotion or anatomy with animal size that were not considered here could affect the scaling of elastic energy storage. For example, significant amounts of elastic energy can be stored in muscle aponeuroses and in the tendinous structures of the trunk (Alexander *et al.* 1985), and the degree to which this occurs might change with size. Secondly, although the assumptions that we have made are supported by the available evidence, one or more of them may in the future be shown to be incorrect. Thirdly, the empirical scaling relationships that we used are likely to differ to some extent from the true relationships because they were calculated using a limited number of species and will incorporate some experimental error.

If experimental evidence confirms that the contribution of elastic energy storage does not increase with size in quadrupedal mammals, then the current understanding of the energetic implications of size must be revised. This would have important implications for muscle energetics. An inability to utilise elastic energy to offset the mechanical work of locomotion could provide a partial explanation for the low locomotor efficiency of small mammals (Biewener *et al.* 1981). However, if the contribution of elastic energy to locomotion in small mammals is the same as or greater than it is in larger species, the muscles of small mammals must be operating even less efficiently than previously thought.

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