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A Biomechanical Investigation into the Absence of Leaping in the Locomotor Repertoire of the Slender Loris (*Loris tardigradus*)

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Key Words

Locomotion · Biomechanics · Leaping · *Loris tardigradus* · *Galago moholi* · Computer simulation

Abstract

Unlike all other primates, members of the subfamily Lorisinae are never seen to leap. To investigate the anatomical specializations that are behind the absence of leaping in their locomotor repertoire, a predictive mechanical model of leaping was developed using the lesser bushbaby, *Galago moholi*, as a size-matched leaping prosimian comparison. This enabled the required limb movements for a leaping slender loris to be calculated, and hence the torque and power requirements at each of the hindlimb joints. From this information, the maximum feasible leap was calculated for the slender loris morphotype, and it was found that this alone would prevent the animal from leaping a greater distance than it could walk over, so that the reduction in fitness due to an apparent loss of leaping from the behavioural repertoire can be considered to be very small.

Introduction

The animal chosen for the investigation into the absence of leaping behaviour among the lorisines is the slender loris, *Loris tardigradus*. This is the smallest of the four species that make up the family Lorisinae and it is found living in dense undergrowth in southern India and Sri Lanka. It is a cryptic animal, eating insects and some fruit [1, 2]. Like all the members of the Lorisidae, it moves in a slow quadrupedal fashion, and is never seen to either leap or gallop [3]. However, 'slow' is a relative term – the movement has been described as a 'racewalk' [4] and the animals can reach a maximum speed of $1.65 \text{ m} \cdot \text{s}^{-1}$ [5]. By comparison, the ground speed of a galago leaping 1 m is approximately $2.2 \text{ m} \cdot \text{s}^{-1}$ [6].

The evolutionary history of the locomotor system in the Lorisidae is unclear; however, their exclusively slow quadrupedal life-style seems likely to be a derived

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character for a number of reasons. Firstly, lorises have a specialized anatomy associated with their quadrupedal life-style, their hand morphology for example [7]. Secondly, the Eocene primate fossil record suggests that ancestral prosimians, whether Adapidae or some other group, were lemur-like, generalized arboreal animals [8], though some of the Adapidae have been described as non-leapers [9]. Thirdly, the ability to leap is widespread among both primates and other arboreal mammals suggesting that this is an ancestral feature, and that the loss of leaping is derived. Ultimately, this apparent loss of leaping from the locomotor repertoire must be due to the evolutionary pressures acting on the animal in its environment. Walking locomotion might be considered more suitable for an animal that spends its time in dense undergrowth where the intersupport distance is low compared to the body size of the animal. However, it is easy to imagine times when the ability to leap would still be beneficial to a slender loris: for example, there will be discontinuities in its substrate that will be too large to simply bridge across, where a leap would save time and/or energy. This paper investigates one of the possible proximate reasons why this does not happen.

One possible hypothesis is that the slender loris is so anatomically specialized as a slow quadrupedal walker that it is unable to leap further than the distance it can stride across and hence encounters no situations where leaping would be a useful option. This paper tests this hypothesis by calculating the maximum distance that a slender loris is mechanically able to leap (should it ever choose to do so): if this distance is reasonably large, then the anatomical specialization hypothesis is unlikely to be true. This paper does not, however, consider whether given anatomical features might improve its performance.

There are a number of approaches available to investigate behaviours that are not normally observed. Often animals can be trained to behave in 'un-natural' manner. For example Japanese macaques, trained to walk on their hindlimbs, have been used to investigate bipedal walking [10]. The main problem with this sort of technique is that the act of training is liable to alter the very anatomy that is being evaluated. Alternatively, abnormal external stimuli can be applied to a non-trained animal in an attempt to elicit the required behaviour. This can either be sensory or by direct motor stimulation. Obviously, this is not an acceptable option with endangered species such as the slender loris.

Another approach is via computer simulation. By creating a predictive leaping model based on static parameters that can be measured on a non-leaping animal, a 'virtual robot' representation can then be made to leap and the mechanical requirements of the action measured. This is the approach followed in this paper.

Materials and Methods

The first step in producing a predictive model is to look at the theoretical mechanics of leaping. Fortunately, leaping as a form of locomotion is mechanically extremely simple (with a few complications). In the first instance the whole animal can be simplified down to a point mass and treated in exactly the same way as a cannonball [11]. The horizontal distance covered is based on two parameters: the take-off angle and the take-off speed. It can be shown, using the standard ballistic equations and ignoring air resistance, that horizontal range can be calculated from the following equation [12]:

$$R = \frac{U^2 \sin 2\theta}{g}$$

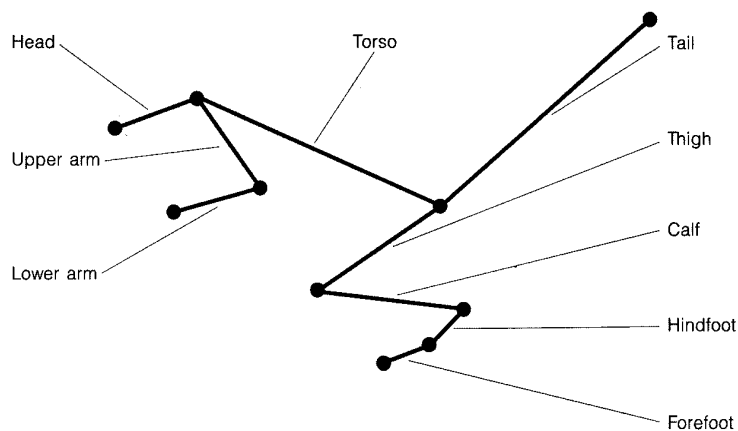


Fig. 1. Diagram showing the segments measured for this study.

where R is the horizontal range (m), U is the take-off speed ($\text{m}\cdot\text{s}^{-1}$), θ is the take-off angle and g is the acceleration due to gravity ($\text{m}\cdot\text{s}^{-2}$).

Therefore leaping a given distance requires the centre of mass to be accelerated to a suitable speed and take-off angle. From the equation, it can also be seen that in order to leap the furthest distance at the lowest speed and hence for the lowest energy cost, the take-off angle needs to be 45° thereby making $\sin 2\theta$ equal to 1 [for discussion see 13]. For long, energetically expensive leaps, this optimal take-off angle is especially desirable.

To model a leap in a slender loris, suitable limb kinematics need to be generated to achieve the required take-off velocity. The leaping kinematics of other prosimian leapers can be used as starting point. The animal chosen for this was *Galago moholi*, the lesser bushbaby. This animal has a very similar size range to a slender loris, is reasonably closely related phylogenetically and spends a large amount of its time leaping [14]. A single animal was filmed leaping various known horizontal distances (0.3–1.4 m, a total of 21 leaps) at the Duke University Primate Center under controlled conditions and the leaping kinematics were analysed using custom-written computer software [13]. These galago leaping kinematics were qualitatively similar to those obtained elsewhere [15, 16] and judged to be representative of a ‘typical’ prosimian leap.

The positions of the major limb joints (fig. 1) were measured for each frame during the take-off stage for a total of 21 leaps over horizontal distances from 0.3 to 1.4 m. The positions of the joint centres are used to define the location of the individual body segments. Each of these body segments has a known centre of mass, and by summing the positions of the segments of mass of each of the body segments, the overall centre of mass for the whole body can be calculated using the following equation [12]:

$$\bar{x}\mathbf{i} + \bar{y}\mathbf{j} = \frac{\sum m_i x_i}{\sum m_i} \mathbf{i} + \frac{\sum m_i y_i}{\sum m_i} \mathbf{j},$$

where \mathbf{i} is the unit vector in the x direction, \mathbf{j} is the unit vector in the y direction, \bar{x} is the x co-ordinate of the centre of mass, \bar{y} is the y co-ordinate of the centre of mass, m_i is the mass of the i th segment and y_i is the y co-ordinate of the i th segment.

Figure 2 shows the position of the overall centre of mass during the first part of a 1.4-metre leap. The centre of mass is accelerated through a straight line at approximately 45° as predicted to minimize energy expenditure.

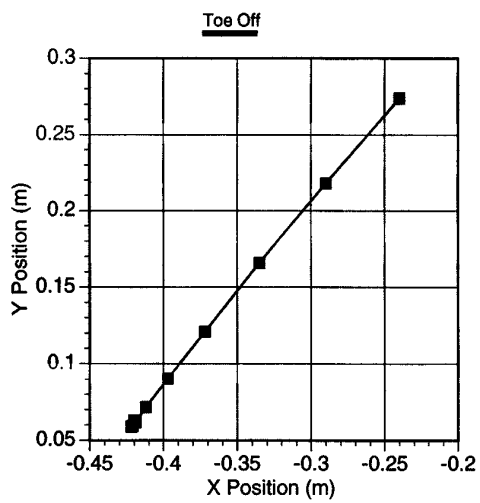


Fig. 2. Graph showing the sequential position of the centre of mass of *G. moholi* at 0.02-second intervals during the take-off phase of a 1.4-metre leap.

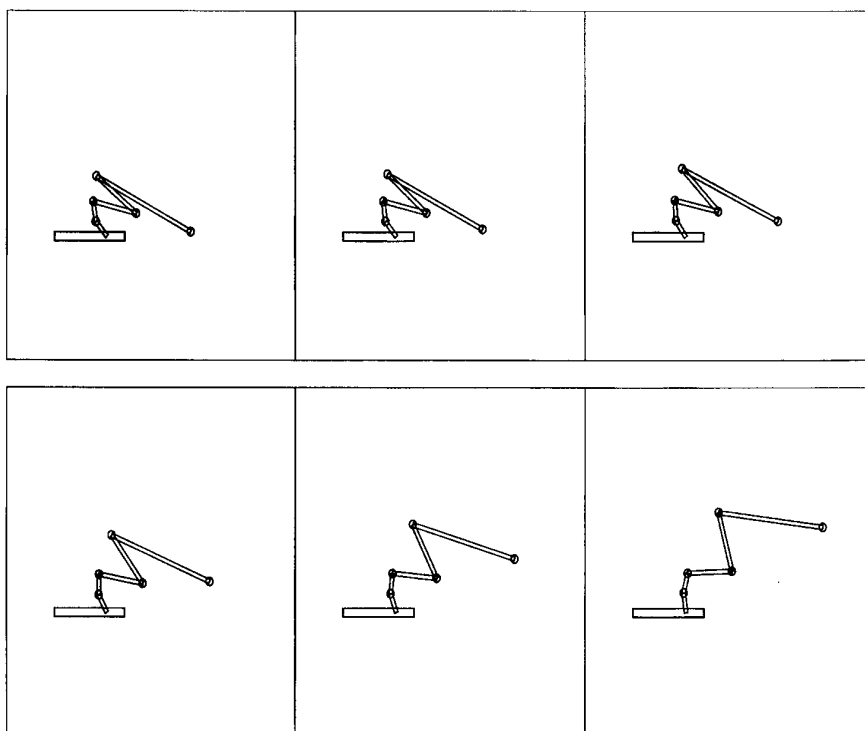


Fig. 3. The segment positions for a 4-metre simulated leap for *G. moholi* as produced by the DADS postprocessor at $t = 0, 0.06, 0.11, 0.17, 0.23, 0.29, 0.34$ and 0.40 s.

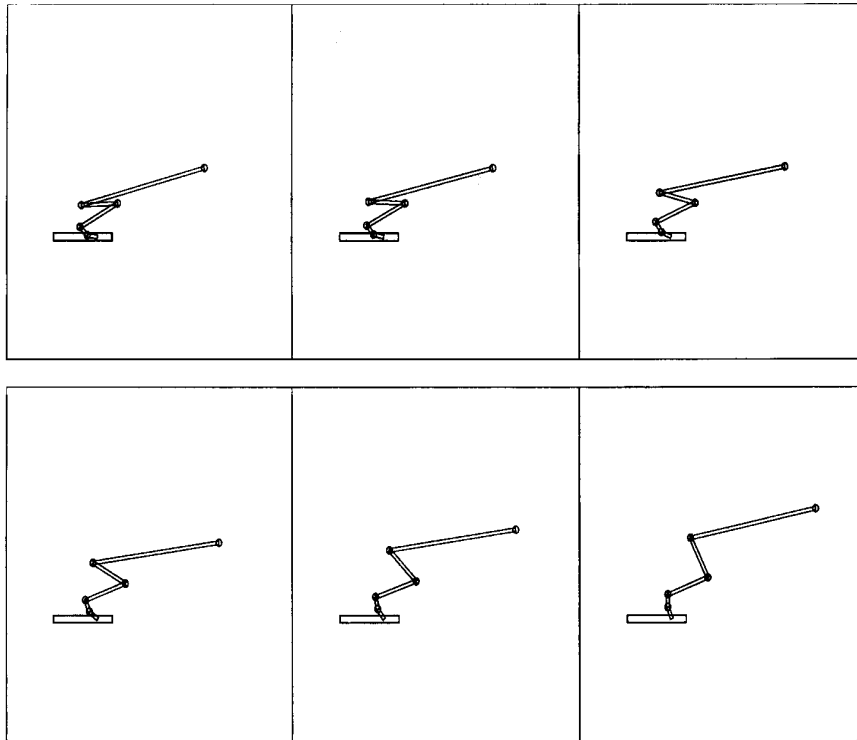


Fig. 4. The segment positions for a 4-metre simulated leap for *L. tardigradus* as produced by the DADS postprocessor at $t = 0, 0.06, 0.11, 0.17, 0.22, 0.28, 0.33$ and 0.39 s.

Table 1. Mass distribution parameters used for the DADS model

Segment	<i>G. moholi</i>			<i>L. tardigradus</i>		
	mass, kg	length, m	MOI, $\text{kg} \cdot \text{m}^2$	mass, kg	length, m	MOI, $\text{kg} \cdot \text{m}^2$
Forefeet	0.005	0.023	2.95×10^{-7}	0.004	0.017	1.69×10^{-7}
Hindfeet	0.003	0.024	1.69×10^{-7}	0.004	0.017	1.69×10^{-7}
Calves	0.017	0.063	5.66×10^{-6}	0.016	0.072	6.91×10^{-6}
Thighs	0.050	0.071	2.33×10^{-5}	0.023	0.062	7.90×10^{-6}
Torso	0.176	0.148	3.34×10^{-4}	0.203	0.215	7.94×10^{-4}

Segment masses taken from Preuschoft et al. [22] and Smith [23] normalized to 0.25 kg and moments of inertia (MOI) calculated assuming cylindrical segments using the equations in Apkarian et al. [24].

The leaping model needs to be able to map the salient features of the galago leap onto the loris morphotype and produce a set of limb movements that will produce the desired leap from the loris virtual robot. There are therefore a number of goals that need to be achieved.

Firstly, the model must produce the correct velocity at take-off (speed and angle). This is an absolute requirement for any object moving along a ballistic trajectory if the effects of air resistance

are ignored. Secondly, the centre of mass should move in a straight line during the take-off phase. This mimics the observed behaviour of the galago during the greater part of take-off and is required to minimize the energy cost of the leap or conversely to maximize the possible horizontal range. Thirdly, leaping must be assumed to be entirely hindlimb driven. This is a necessary simplification in modelling terms to reduce the degrees of freedom to a reasonable level and is certainly a reasonable assumption in *G. moholi* as indicated by recorded kinematics [15] and the hindlimb specializations in both the skeletal [17] and muscular anatomy [18]. In addition, the acceleration of the overall centre of mass was considered to be constant during take-off: again a necessary simplification to reduce calculation times. *Galago* leaping mechanics are obviously considerably more complex than those used for the model (see Günther et al. [19] for a detailed description of results obtained using a force plate; the early and late stages of take-off show non-linear motion of the body centre of mass, for example): simplifications, in terms of assuming mathematical functions for trajectory and acceleration are necessary compromises to allow computer simulation.

The start position was obtained by measuring the observed start position of the lesser bushbaby and fitting the loris segment model to these positions by copying the joint angles and then rotating the overall model so that the line of action of the thrust vector was 45°. The end position was taken as 80% of full hindlimb extension with the model again rotated so that the line of action of the thrust vector was 45°. The 80% extension matches approximately the hindlimb extensions observed at toe-off, although this value is fairly approximate since the instant of toe-off is necessarily rather imprecise due to the relatively low framing rate obtained using a video-based kinematic analysis system.

With known start and end positions and velocities for the centre of mass, and assuming constant acceleration, the position of the overall centre of mass can be calculated for any required moment during the take-off phase using the standard constant acceleration formulae [12]. However, the exact position of the overall centre of mass depends on the positions of the individual segments which obviously vary as the hindlimb extends during take-off. This problem was solved numerically by incrementally increasing the degree of extension at all the hindlimb joints from their start position to their end position and then making small adjustments to the rotation of the whole model to keep the centre of mass on the 45° straight line trajectory. This produces a large set of joint angles that correspond to particular centre of mass positions and hence times after take-off. The computer program then selects 1,000 sets of joint positions evenly distributed in time throughout the take-off phase. These are then fed into a morphologically identical model in a commercial dynamic analysis package, DADS [20], which was used to calculate the forces and torques acting about the joints of the model (for a discussion of multibody modelling, see van den Bogert and Schamhardt [21]). Table 1 shows the segment data used for the DADS model. Figures 3 and 4 show frames from the animation output from the DADS postprocessor. These figures show that the model is at least qualitatively valid.

Results

The model was used to simulate leaps for the two different animals using their different static parameters. Figure 5 shows the comparison of the segment lengths for the two animals. As can be seen, there is very little difference: *L. tardigradus* has a longer torso and also its thigh length is shorter than its calf length. *G. moholi* has appreciably longer feet, both proximal and distal to the mid-tarsal joint. Figure 6 shows the segment masses for the two species normalized to that the total body mass for both is 0.25 kg. The most obvious difference in this figure is the very much heavier thigh compartment in the galago: 20% of the body mass is contained in this segment. Figure 7 shows the segment cross-sectional area. This shows a very similar picture to figure 6 with a very large cross-section for the *G. moholi* thigh segment. *L. tardigradus* has a large cross-sectional area for its feet (recalling the importance of a strong grip in these animals).

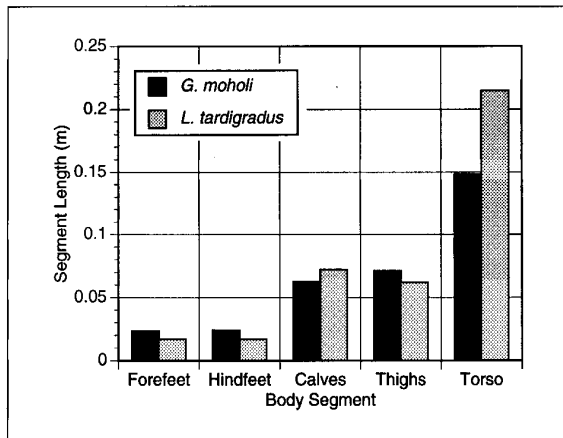


Fig. 5. Graph showing the measured segment lengths for *G. moholi* and *L. tardigradus*.

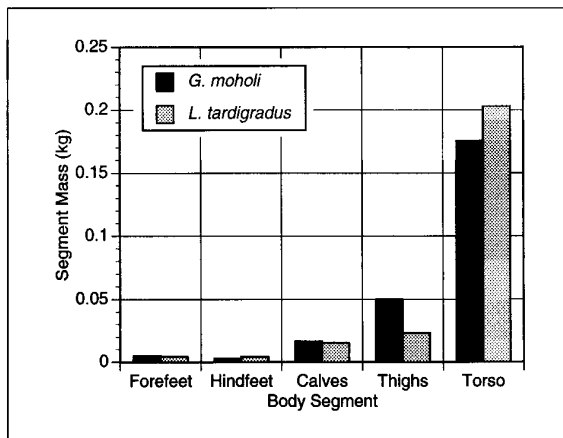


Fig. 6. Graph comparing the segment masses of *G. moholi* and *L. tardigradus*. Data taken from Preuschoft et al. [22] and Smith [23] normalized to 0.25 kg.

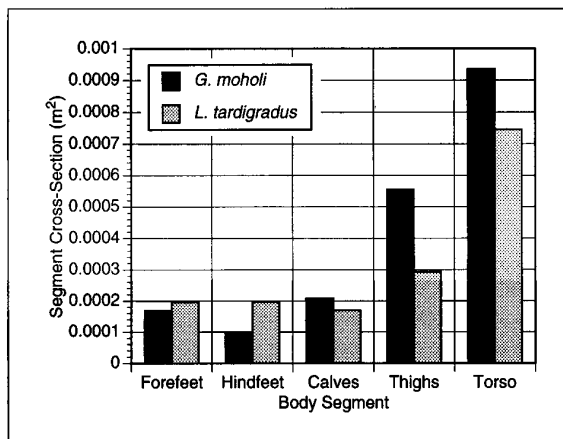


Fig. 7. Relative cross-sectional area of the body segments for *G. moholi* and *L. tardigradus*. This shows an average value obtained by dividing the segment mass by the segment length.

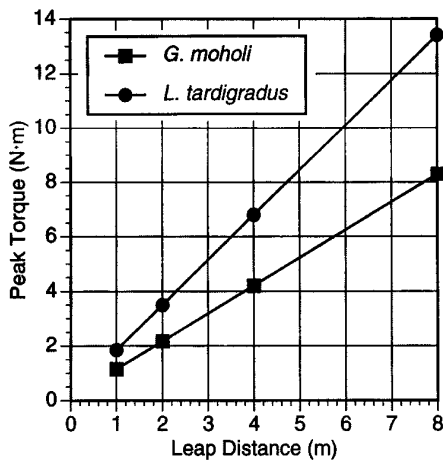


Fig. 8. Graph showing the peak torque required around the hip joint as a function of the leap distance used in the model for both *G. moholi* and *L. tardigradus*.

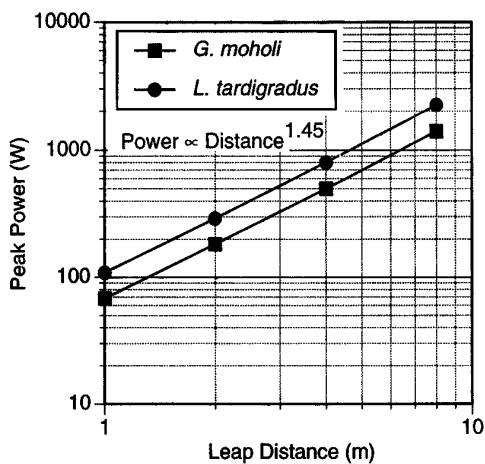


Fig. 9. Graph showing the peak power required around the hip joint as a function of the leap distance used in the model for both *G. moholi* and *L. tardigradus*.

The model was used to simulate a variety of leap distances (1, 2, 4 and 8 m) and used to calculate the peak torques and peak powers required around each joint. Figure 8 shows the effect of leap distance on the peak torque required. Figure 9 shows the effect of leap distance on the maximum power required. As can be seen, the relationship is linear between peak torque and leap distance, but depends on distance^{1.45} for peak power.

For the subsequent comparisons, the distance chosen for the simulated jump was 4 m. 4 m is a relatively long jump for a galago though possibly not its maximum – it is very difficult to know what is the maximum distance *G. moholi* can leap. Leaps of

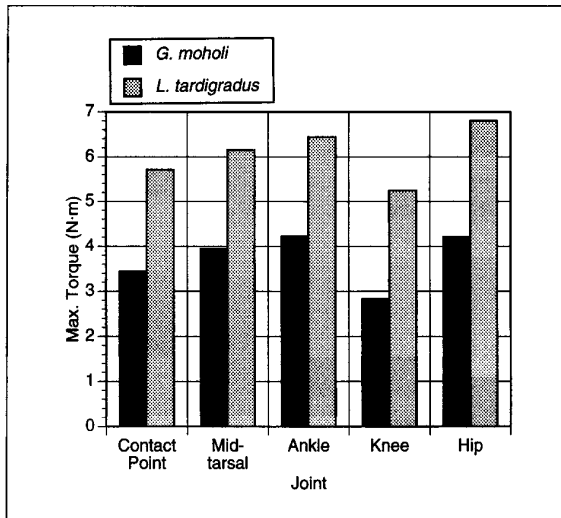


Fig. 10. Graph showing the maximum torque required around the various joints for a simulated 4-metre leap for *G. moholi* and *L. tardigradus*.

8 m have been reported, but these are from observations in the wild so that the distances quoted are generally very much approximate, and in most cases the change in height is not known [25]. In addition, bushbabies are thought to use a 'springboarding' technique for their longest leaps [19], bouncing onto the substrate to store up energy for the subsequent leap. 4 m is probably a reasonable estimate of the longest distance that an animal would leap without the aid of an external energy store.

Figure 10 shows the maximum torque that needs to be generated about the joints in the model. This figure shows that the peak torques required by *L. tardigradus* at all the joints are appreciably higher than those for *G. moholi*. However, this is only indicative of the forces that the muscles need to generate: torque is calculated as the force multiplied by the distance away from the centre of rotation. By moving the insertion point of its tendon further from the joint centre, the torque generated by a muscle can be increased without increasing the force. However, there are limits to this, especially for muscles extending the limb since the determinant is on the closest distance between the tendon and the joint centre. Also, there is a limit to how much a given muscle can contract. If the amount of leverage is increased, then the degree of contraction for a given angular excursion increases. So, although there is no hard and fast relationship, the joint torque is a reasonable indicator of the relative muscle force needed.

Figure 11 shows the maximum power required. Again the values for *L. tardigradus* are higher than their equivalents for *G. moholi*. It is important to note that the values for the contact point and the knee are negative. This is an indication that the peak power requirement around these joints occurs when they are doing negative work, where movement around the joint is in the opposite direction to the torque applied. The negative work at the contact point is probably a consequence of the friction between the foot and the substrate. Work is necessary about the knee joint to slow its extension to keep the centre of mass moving on the desired path.

These results show that *L. tardigradus* is indeed less well designed for leaping, but the differences are still small. The most limiting is the knee torque which is almost

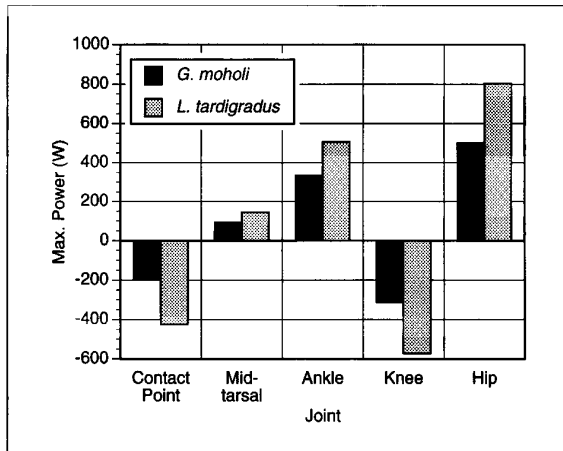


Fig. 11. Graph showing the maximum power that needs to be generated about the joints for a simulated 4-metre leap in *G. moholi* and *L. tardigradus*.

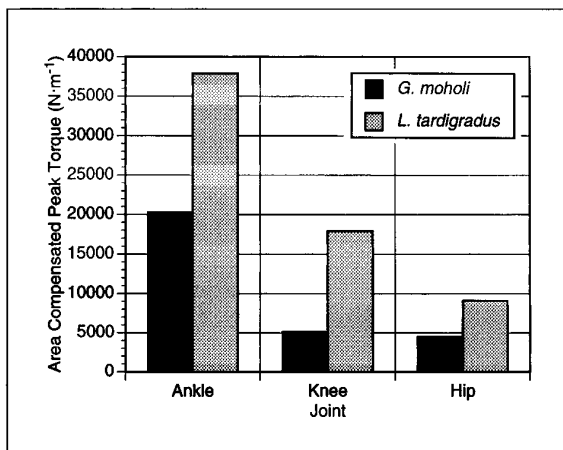


Fig. 12. Graph showing the relative area-compensated torque for a 4-metre simulated leap in *G. moholi* and *L. tardigradus*.

double that of *G. moholi*. However, the maximum torque is dependent on the cross-sectional area, and the maximum power is dependent on the mass. If a number of simplifications are made, this can be taken into consideration. It is impossible, as yet, to know the contributions of the different muscles to the torques and powers at the joints. However, it seems reasonable, as a first approximation, to assume that ankle extension is mostly powered by muscles in the calf, knee extension by thigh muscles and hip extension by torso muscles (this approximation is least valid for hip extension since it ignores the role of the hamstring muscles and overemphasizes the role of the gluteals; however, without more detailed information on the contributions of individual muscle groups it is difficult to improve upon). Figure 12 shows the results of using this approach for compensating for the segment cross-sectional area.

After this area compensation, there are much bigger differences: between three and four times lower values for *G. moholi*, especially in the knee region. Given the

Fig. 13. Graph showing the relative mass-compensated peak power requirement for a 4-metre simulated leap in *G. moholi* and *L. tardigradus*.

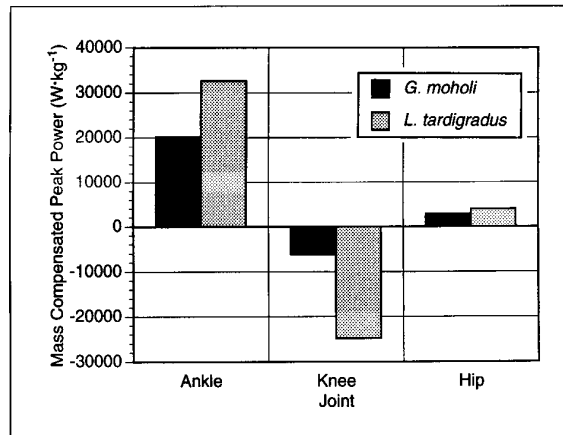


Table 2. Effective power and force contribution that could be expected from an equivalent amount of hind-limb muscle for a galago and for a loris

	Lesser bushbaby	Slow loris
Fibres		
FG, %	37	0
FOG, %	42	44
SO, %	16	53
Force contribution		
FG	2237	0
FOG	841	882
SO	82	266
Total	3160	1147
Effect, %	100	36
Power contribution		
FG	66	0
FOG	21	22
SO	1	4
Total	88	26
Effect, %	100	29

Data derived from Sickles and Pinkstaff [26] and Burke et al. [27]. FG = Fast-twitch glycolytic; FOG = fast-twitch oxidative glycolytic; SO = slow oxidative.

linear relationship between peak torque and leap distance, this would suggest that *L. tardigradus* could leap perhaps 1 m. Figure 13 shows a similar picture for mass-compensated power. There is a fourfold reduction in the power requirement for *G. moholi* in the knee region. Given the non-linear relationship between distance and peak power requirement, this fourfold reduction would suggest that the loris could leap approximately one third ($0.33^{1.45} \approx 0.2$) as far as the bushbaby – perhaps 1.3 m.

However, these relationships do not take into account the difference in muscle fibre types between the two animals. Table 2 shows the expected differences in the

maximum power and force that can be generated by a similar muscle in a bushbaby and a loris. The percentage effect values in the table are calculated from the reported maximum tetanic force for the given muscle types and the twitch times. The magnitude of the differences due to muscle fibre type are in some doubt [see 28 for discussion], but this table does give some approximate figures. For both peak power and force, loris type musculature is likely to be about one third as effective (as far as leaping is concerned) as bushbaby type musculature. This would reduce the expected maximum jump for the simulated *L. tardigradus* by a further two thirds to approximately 0.3 m.

Discussion

The prediction that the maximum leap distance for a slender loris would be around 0.3 m goes a considerable way towards explaining one of the proximate reasons why this behaviour is never seen. Earlier in this paper I argued that there were circumstances when it might be beneficial for a loris to be able to leap across discontinuities in the substrate. However, these circumstances largely disappear when we find that the maximum leap that the animal can perform due to the constraints of its anatomy is very little (if at all) more than the maximum gap it can bridge across. If it encounters discontinuities in its substrate that are larger, then its extreme anatomical specializations for slow quadrupedal locomotion are such that it has no choice but to find a way around. It is mechanically unable to perform in any other way.

The validity of this conclusion depends greatly on the validity of the model used. The predictive leaping model presented here is necessarily basic in its approach and makes a number of assumptions and simplifications. The derivation of kinetic data from the inverse dynamic analysis of the kinematics of a rigid segment model has been used for a number of years and has some well-known shortcomings [29, 30]; however, within its limitations, it is a reliable technique [31]. The generation of the kinetic data in the first place is much more problematical. No attempt has been made to justify the biology behind the set of movements generated by the leaping model. Rather, a set of goals has been formulated from mechanical principles and the model has been made to fit the mechanical constraints. The model is correct in that it demonstrates how the limbs could move to elicit the required jump, but it cannot be expected to produce the exact movements seen. The model selects a set of limb movements that fulfil the mechanical requirements and minimizes extraneous movements so that the kinetics it chooses should be close to optimal.

There is scope for specific improvements in the model. The constant force function could be changed to a function that more closely mimics the force seen to be exerted on the substrate by a leaping prosimian. However, this would need to be altered in a complex fashion dependent on the distance to be leapt. In addition, the algorithm used for extending the hindlimb could be altered so that the rate of extension could be varied throughout the take-off phase at the different joints. This may well have a significant effect on the peak forces required and which joints they need to act upon. In addition, the analysis could be improved to look at idealized linear tensile force generators connected around the joints rather than abstract torque-generating engines. This could give much better information on the location of the force-generating segments and could also be extended to look at the possible effects of two joint

muscles. In addition, the latest versions of dynamic analysis programs allow their output data sets to be read directly by finite element packages so that the dynamic stresses on the bones could also be calculated.

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