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Leg design and jumping technique for humans, other vertebrates and insects

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SUMMARY

Humans, bushbabies, frogs, locusts, fleas and other animals jump by rapidly extending a pair of legs. Mathematical models are used to investigate the effect muscle properties, leg design and jumping technique have on jump height. Jump height increases with increased isometric force exerted by leg muscles, their maximum shortening speeds and their series compliances. When ground forces are small multiples of body mass (as for humans), countermovement and catapult jumps are about equally high, and both are much better than squat jumps. Vertebrates have not evolved catapult mechanisms and use countermovement jumps instead. When ground forces are large multiples of body mass, catapult jumps (as used by locusts and fleas) are much higher than the other styles of jump could be. Increasing leg mass reduces jump height, but the proximal-to-distal distribution of leg mass has only a minor effect. Longer legs make higher jumps possible and additional leg segments, such as the elongated tarsi of bushbabies and frogs, increase jump height even if overall leg length remains unchanged. The effects of muscle moment arms that change as the leg extends, and of legs designed to work over different ranges of joint angle, are investigated.

1. INTRODUCTION

A wide variety of animals, including humans, make standing jumps by rapidly extending a pair of legs. Species that have been studied include fleas (Bennet-Clark & Lucey 1967), locusts (Bennet-Clark 1975), frogs (Calow & Alexander 1973; Hirano & Rome 1984; Lutz & Rome 1994) bushbabies and other prosimians (Günther 1985; Günther *et al.* 1991) and humans (Bobbert & van Ingen Schenau 1988; Pandy *et al.* 1990; Dowling & Varmos 1993). Recognized adaptations for jumping include long, muscular legs, sometimes with additional segments formed by elongation of tarsal bones (frogs, bushbabies) or by mobility of the sacro-iliac joint (frogs) (Emerson 1985). At least two techniques are used to improve jumping performance by taking advantage of elastic elements in series with the muscles. Humans make a countermovement, bending the legs immediately before extending them. Komi & Bosco (1978) have shown that this enables them to jump higher than they otherwise could. Jumping insects use catapult mechanisms, storing elastic strain energy and then releasing it suddenly to power the jump (Bennet-Clark 1976). Bennet-Clark & Lucey (1967) showed that the jumps of small insects require much higher power outputs per unit mass than any known muscle can provide. Catapult mechanisms enable work done relatively slowly by muscles to be released much more rapidly at take-off.

The aim of this paper is to improve our understanding of leg design in jumping animals and of the techniques used for standing jumps. How does jump performance depend on muscle properties, on the distribution of mass in the legs and on the number of

leg segments? To what angle should the joints bend, in preparation for a jump? Can an advantage be gained by having muscles whose moment arms change, as the joint extends? In what circumstances can a countermovement improve a jump and when will a catapult mechanism be more effective?

These questions will be tackled by mathematical modelling. A model will be described that is general enough to be applied to jumpers of all sizes and taxa; from fleas to humans. Muscle properties, other aspects of leg design and jumping technique will be varied and the effects on jump height determined. Only vertical jumps will be considered.

2. THEORY

(a) *Model with two leg segments*

The model used for most of the calculations is shown in figure 1*a*. It jumps by extending its legs. The jump is powered by knee extensor muscles which exert equal moments about the two knees: the properties of these muscles are described in §2*c*. The model starts from rest and its symmetry ensures that the jump is vertical.

Each leg consists of two segments, each of length s . The point of contact of each foot with the ground is vertically below the corresponding hip, and at time t the angle of each knee is 2θ . The hips are at height y from the ground and the knees are x lateral to them. Thus

$$y = 2s \cdot \sin \theta, \quad (1)$$

$$y = 2s\dot{\theta} \cdot \cos \theta, \quad (2)$$

$$x = s \cdot \cos \theta, \quad (3)$$

$$x = -s\dot{\theta} \cdot \sin \theta = -\frac{1}{2}\dot{y} \cdot \tan \theta, \quad (4)$$

$$\text{and from equation } 2\dot{\theta} = (\dot{y} \cdot \sec \theta)/2s. \quad (5)$$

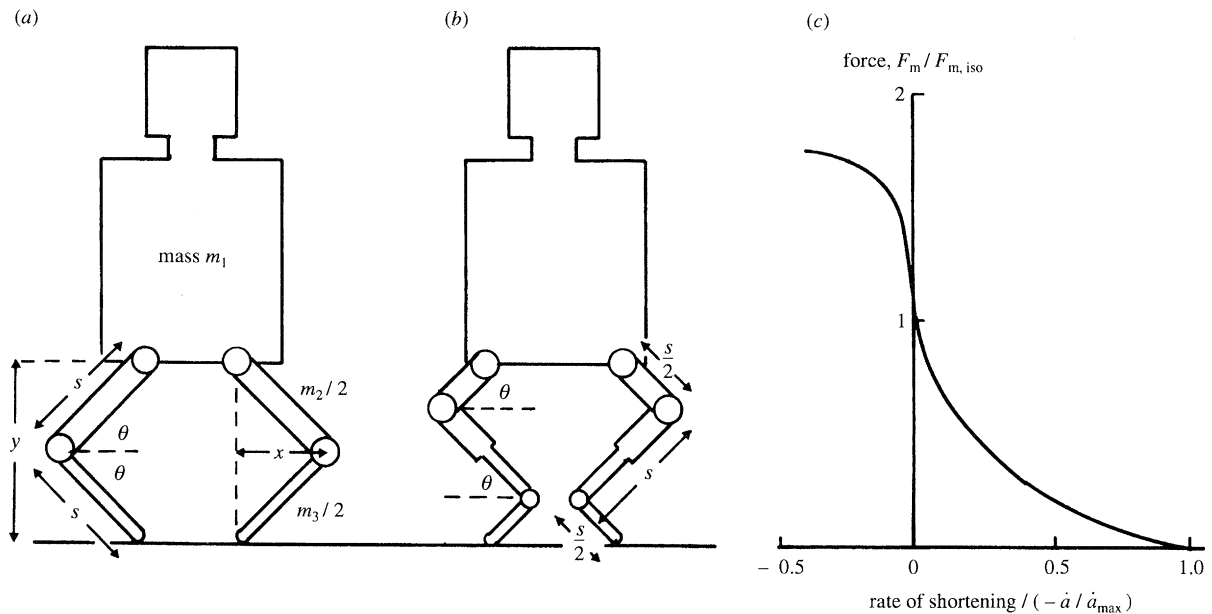


Figure 1. Models of bipedal jumpers with: (a) two segments; and (b) three segments in each leg. (c) The force-velocity relationship for the models' muscles, described by equations (22). The force is expressed as a multiple of the isometric force (i.e. as $F_m/F_{m,iso}$) and the rate of shortening as a multiple of the maximum shortening speed (as $-\dot{a}/\dot{a}_{max}$).

We will obtain an equation of motion by considering energy balance. At time t , the knee muscles are exerting moments T about the knees, each of which is extending at a rate $2\dot{\theta}$. The rate at which the knee muscles are doing work must equal the sum of the rates of increase of the potential energy P and kinetic energy K of the model

$$4T\dot{\theta} = \dot{P} + \dot{K}. \quad (6)$$

The trunk has mass m_1 , the two thighs together m_2 and the two lower legs together m_3 . Each leg segment is a uniform rod, so its centre of mass is midway along its length. Thus these centres of mass are at heights $3y/4, y/4$, and the potential energy of the model is

$$P = (gy/4)(4m_1 + 3m_2 + m_3), \quad (7)$$

(g is the gravitational acceleration). The equation implies that the centre of mass of the trunk is at the height of the hip joints, but this assumption has no effect on the analysis because we will be using the derivative of the potential energy, rather than the potential energy itself.

The trunk moves vertically with velocity \dot{y} . The centres of mass of the thighs and lower legs have vertical components of velocity $3\dot{y}/4, \dot{y}/4$ and horizontal components $\pm\dot{x}/2, \pm\dot{x}/2$. Each thigh has moment of inertia $m_2 s^2/24$ about its centre of mass, and angular velocity $\pm\dot{\theta}$; and each lower leg has moment of inertia $m_3 s^2/24$ and the same angular velocity. Thus the total kinetic energy of the model is

$$K = (\dot{y}^2/32)(16m_1 + 9m_2 + m_3) + (\dot{x}^2/8)(m_2 + m_3) + (s^2\dot{\theta}^2/24)(m_2 + m_3), \quad (8)$$

(using equations (4) and (5) to substitute for \dot{x} and $\dot{\theta}$ and remembering that $\sec^2\theta = 1 + \tan^2\theta$)

It will be convenient to write

$$m_4 = m_2 + m_3, \quad (9)$$

$$m_5 = 4m_1 + 3m_2 + m_3, \quad (10)$$

$$m_6 = 12m_1 + 7m_2 + m_3, \quad (11)$$

so that equations (7) and (8) become

$$P = gym_5/4, \quad (12)$$

$$K = (\dot{y}^2/24)(m_6 + m_4 \tan^2\theta). \quad (13)$$

By differentiating with respect to time

$$\dot{P} = g\dot{y}m_5/4, \quad (14)$$

$$\dot{K} = (\dot{y}\dot{y}/12)(m_6 + m_4 \tan^2\theta) + (\dot{y}^2/24)(2m_4\dot{\theta} \tan\theta \sec^2\theta). \quad (15)$$

By substituting equations (14) and (15) in (6), and using (5) to eliminate $\dot{\theta}$

$$2T \sec\theta/s = gm_5/4 + (\dot{y}/12)(m_6 + m_4 \tan^2\theta) + (m_4 \dot{y}^2/24s) \tan\theta \sec^3\theta, \quad (16)$$

This equation is used to calculate the motion of the model during take-off. The height y of the hips is obtained by numerical integration and from it the knee angle 2θ by using equation (1). The force F_g on the ground is the sum of the weight of the body and the forces needed to give the segments their vertical components of acceleration

$$F_g = mg + m_5 \dot{y}/4, \quad (17)$$

where m is the total mass of the body

$$m = m_1 + m_2 + m_3. \quad (18)$$

When $y > 2s$ or $F_g < 0$, the feet have left the ground. At the instant when they leave the ground, $y = y_{off}$ and $\dot{y} = \dot{y}_{off}$. The centre of mass of the model is then rising at a rate $m_5 \dot{y}_{off}/4m$ (this is \dot{P}/mg , equation (14)). A projectile fired vertically with velocity v rises to a height $v^2/2g$, so the centre of mass will rise by $m_5^2 \dot{y}_{off}^2/32m^2g$ after the feet have left the ground. If the

joints remained fixed at the angles they had when the feet left the ground, the hips would rise to a height $y_{\text{off}} + m_5^2 \dot{y}_{\text{off}}^2 / 32m^2g$ at the peak of the jump. However, they will rise a little higher if the legs become completely straight, moving the centres of mass of thighs and lower legs distances $(2s - y_{\text{off}})/4$ and $3(2s - y_{\text{off}})/4$ further below the hips. Thus the difference of height between the hips and the centre of mass of the whole body is increased by $(m_2 + 3m_3)(2s - y_{\text{off}})/4m$. The height of the jump, defined as the height of the hip joints above the ground at the peak of the jump, is thus

$$h = y_{\text{off}} + (m_5^2 \dot{y}_{\text{off}}^2 / 32m^2g) + (m_2 + 3m_3)(2s - y_{\text{off}})/4m. \quad (19)$$

(b) Model with three leg segments

Some calculations will be presented for the model shown in figure 1*b*, which has three segments in each leg instead of two. These are a thigh of length $s/2$, a shank of length s and a metatarsal segment of length $s/2$. The distribution of mass along the length of the leg is the same as for the previous model; thus the thigh and metatarsal segment are uniform rods of masses $m_2/4, m_3/4$ and the shank consists of two uniform rods, each of length $s/2$, joined end to end; the proximal half of the shank has mass $m_2/4$ and the distal half $m_3/4$.

The two joints in each leg are constrained always to have equal angles, perhaps by a parallel rule mechanism (not represented in the diagram). The muscular moment T may all be applied at one of the joints, in which case a moment is transmitted to the other by the linking mechanism. Alternatively, moments totalling T may be applied to the two joints by separate muscles. The mathematical analysis is the same, in either case.

The equation of motion can be obtained by a similar argument to the one presented for the model with only two leg segments, in §2*a*. The more concise argument that follows leads to the same conclusion.

Mass in this model is distributed over height in precisely the same way as in the previous model, so at any given hip height y the potential energies of the two models are equal. Also, at any given hip velocity \dot{y} the vertical components of velocity of particles in corresponding positions in the two models are equal: therefore, the kinetic energies associated with vertical components of velocity are equal. However, particles in the legs of this model are on average only half as far from the vertical line from hip to foot, as in the other model. Therefore the transverse displacements that occur as the leg straightens are halved, transverse components of velocity are halved and kinetic energies associated with transverse components of velocity are only one quarter as much as in the previous model. In equation (13), these kinetic energies are represented by the term in m_4 . It follows that we can obtain the equation of motion for the model with three segments in each leg by dividing by four those terms in equation (16) which include m_4 . Equivalently, we can multiply by four the terms on the right which do not include m_4

$$\ddot{y} = (192T \sec \theta - 24m_5 g s - m_4 y^2 \tan \theta \sec^3 \theta) / [2s(4m_6 + m_4 \tan^2 \theta)]. \quad (20)$$

(c) Muscle properties

The extensor muscle which powers the jump consists of a contractile element in series with an elastic element. Any change $\delta\theta$ in the half-angle of the knee requires a change $2r \cdot \delta\theta$ in the overall length of the muscle, where r is the moment arm of the muscle about the joint. This is the sum of length changes δa in the contractile element and δb in the elastic element.

$$2r \cdot \delta\theta = \delta a + \delta b. \quad (21)$$

The contractile element has force-velocity properties expected to be realistic for striated muscle. More specifically, the force F_m that the muscle exerts is related to the rate of change of length \dot{a} of the contractile element

for $-\dot{a} < 0$

$$F_m = F_{m,\text{iso}} [1.8 - 0.8(\dot{a}_{\text{max}} - \dot{a}) / (\dot{a}_{\text{max}} + 23\dot{a})], \quad (22a)$$

for $0 < -\dot{a} < \dot{a}_{\text{max}}$

$$F_m = F_{m,\text{iso}} (\dot{a}_{\text{max}} + \dot{a}) / (\dot{a}_{\text{max}} - 3\dot{a}), \quad (22b)$$

for $-\dot{a} > \dot{a}_{\text{max}}$ $F_m = 0$, (22c)

(see figure 1*c*). Here $F_{m,\text{iso}}$ is the force exerted in isometric contraction and \dot{a}_{max} is the maximum rate of shortening of the contractile element. Equation (22*b*) is Hill's (1938) equation for muscle shortening, with some signs changed because shortening is a negative length change. Similarly, equation (22*a*) is Otten's (1987) equation for stretching of active muscle. In these equations, the constant describing the curvature of the force-velocity relationship (a/P_0 in Woledge *et al.* 1985; k in Otten 1987) is given the value 0.33. This value is typical for fast skeletal muscle (Woledge *et al.* 1985).

The elastic element is a linear spring of compliance C , which undergoes extension b when force F_m acts on it

$$F_m = b/C. \quad (23)$$

At every stage in take-off, the forces given by equations (22) and (23) must be equal.

We will see, in section 5(*a*), how forcible stretching of the muscle in a countermovement can enable it to exert increased force in a subsequent contraction. This results from interaction of the series compliance with the force-velocity properties of the contractile elements. No attempt is made in the model to reproduce an additional effect of an initial stretch, 'potentiation' of the contractile machinery itself. This effect seems relatively unimportant (Ettema *et al.* 1990).

The moment arm r is related to the angle 2θ of the joint by the equation

$$r = r_0 [1 + (6k/\pi)(\theta - \pi/3)]. \quad (24)$$

When $k = 0$ (as in most of the calculations that will be presented) the moment arm has a constant value r_0 . When it has other values, the moment arm changes linearly from $(1 - k)r_0$ when $\theta = \pi/6$ to $(1 + k)r_0$ when $\theta = \pi/2$. Note that the mean moment arm, over this range, is always r_0 . In most of the simulations presented in this paper, including all those in which r varies, the minimum value of θ is $\pi/6$. When the leg is fully extended, $\theta = \pi/2$.

The moment T exerted by the extensor muscle about the joint is

$$T = F_m r. \quad (25)$$

3. COMPUTATION

The equations given above were incorporated in a program run on a desk-top computer. This simulated jumps starting from rest, following the model's movements by numerical integration until the feet left the ground. Equation (16) or (20), as appropriate, was used to calculate the changes of velocity \dot{y} and hip height y during each time increment. Hence joint angle was calculated using equation (1). The increment of joint angle was partitioned between the contractile and series elastic elements of the muscle by stipulating that the muscle forces given by equations (22) and (23) must remain equal. The force so obtained was used as the muscle force for the next time increment.

Integration ceased when the force on the ground (equation (17)) fell to zero. The height of the jump was then calculated, using equation (19). Halving the time increments in a sample of runs altered jump heights by less than 1%.

Simulations were performed for three jumping techniques. In the following description, $2\theta_{\min}$ is the minimum angle to which the knee bends in preparation for the jump.

1. *Squat jumps*. The simulation starts at rest, with knee angle $2\theta_{\min}$. Initially force F_m is zero and the knee is prevented from bending further by a passive stop as occurs, for example, when a person is squatting with the posterior surface of the thigh resting on the calf. The muscle is activated and contracts, stretching the series elastic elements and building up a moment. No movement occurs until the acceleration given by equation (16) or (20) becomes positive, at which instant the legs start extending.

2. *Catapult jumps*. Again, the model is initially at rest with knee angle $2\theta_{\min}$. The muscle is active, exerting its isometric force $F_{m,iso}$, but the joint is prevented from extending by some other means. For example, the knee extensor muscle in locusts develops tension prior to a jump, while extension is prevented by an antagonist (Bennet-Clark 1975). The joint is suddenly released (in locusts, the antagonist relaxes very rapidly) and take-off starts.

3. *Countermovement jumps*. The model is initially at rest with the legs straight and the muscle inactive. It falls for a while under gravity according to equation (16) or (20), with F_m fixed at zero. At some stage during its fall, the muscle is suddenly activated. A moment is developed at the knee, decelerating the fall and then accelerating the model upwards to take off. The time at which the muscles are activated is varied in successive trials to find by trial and error the time required to make the minimum knee angle reached in the simulation equal the chosen value $2\theta_{\min}$.

The results obtained in this study will be presented in dimensionless form using body mass m as the unit of mass, leg segment length s as the unit of length and gravitational acceleration g as the unit of acceleration.

Thus the unit of time is $(s/g)^{1/2}$. The following parameters will be used to describe muscle properties:

the isometric force parameter

$$\hat{F}_{m,iso} = F_{m,iso} r_o / mgs, \quad (26)$$

the shortening speed parameter

$$\hat{a}_{max} = (\dot{a}_{max} / r_o) (s/g)^{1/2}, \quad (27)$$

and the compliance parameter

$$\hat{C} = CF_{m,iso} / r_o. \quad (28)$$

4. VALUES FOR PARAMETERS

The models presented in this paper are designed to throw light on jumping by animals ranging from humans to small insects. Our choice of parameters will be guided principally by data for humans (body mass approximately 70 kg), bushbabies (*Galago senegalensis* and *moholi*, 0.3 kg) and locusts (*Schistocerca gregaria*, 2 g).

The total mass of the two thighs is 20% of body mass both in humans and in *Galago* (Winter 1990; Grand 1977). The mass of the two lower legs and feet is 12% of body mass in humans and 10% in *Galago* (same sources). A reasonably realistic model of jumping mammals can therefore be obtained by taking $m_1 = 0.7m$, $m_2 = 0.2m$ and $m_3 = 0.1m$; these segment masses have been used except where it is stated otherwise. Note, however, that at least some insects have relatively lighter legs. The two femora of *Schistocerca* total only 14% of body mass and the two tibiae and tarsi only 3% (Bennet-Clark 1975).

The minimum knee angle, in the countermovement prior to jumping, is about 75° in humans (Bobbert & Van Ingen Schenau 1988) and 30° in *Galago* (Günther 1985). An intermediate value of 60° will be used as the minimum knee angle ($2\theta_{\min}$) in this study, except when the effects of varying this angle are being investigated. Note that the chosen angle is much too large to be realistic for *Schistocerca*, which bends the knee almost to 0° in preparation for jumping (Heitler 1977).

Peak ground forces in standing jumps are generally 2–3 times body mass for humans (Dowling & Vamos 1993), up to 13 times body weight in *Galago* (Günther 1985), about 18 times body weight in *Schistocerca* (Bennet-Clark 1975) and up to at least 135 times body weight in fleas (Bennet-Clark & Lucey 1967). Isometric force parameters $F_{m,iso}$ of one, five and 25, respectively, will be used in simulations designed to represent jumps by humans, bushbabies and insects. When the muscles exert these forces at knee angles (2θ) of 60°, the ground forces (exerted by the two feet together) are 2.3, 12 and 58 times body weight, respectively. The peak forces exerted in simulated jumps may be somewhat more or less than these values, depending on the jumping technique (see figure 2).

Maximum shortening speeds of muscles are usually expressed in terms of muscle fascicle lengths per second. To select realistic values of \dot{a}_{max} for investigation, we must first estimate the resting length of the muscle fascicles. In most of the simulations, the knee will extend from a minimum angle of 60° so its working range, from the minimum to full extension, is 120° or

2.1 radians. A muscle with a moment arm r_0 , moving the joint through that angular range, must shorten by $2.1 r_0$. Studies of rabbit leg muscles (Dimery 1985) and bird wing muscles (Cutts 1986) indicate that the working range of length of muscles is commonly about one quarter of the resting length, so a muscle required to shorten by $2.1 r_0$ can be expected to have fascicles about $8.4 r_0$ long. For a muscle shortening at $\dot{\epsilon}$ lengths per second, the shortening speed can thus be estimated as $8.4 r_0 \dot{\epsilon}$.

In this paper, muscle shortening speeds are represented by the dimensionless parameter $(\dot{a}/r_0)(s/g)^{\frac{1}{2}}$ which, by the argument of the previous paragraph, equals $8.4\dot{\epsilon}(s/g)^{\frac{1}{2}}$. Leg segment length s would be about 450 mm for humans, 66 mm for *Galago* (Grand 1977) and 25 mm for *Schistocerca* (Bennet-Clark 1975). The corresponding values of $(s/g)^{\frac{1}{2}}$ are 0.21 s for humans, 0.08 s for *Galago* and 0.05 s for *Schistocerca*.

The maximum shortening speed for fast fibres from human deltoid muscles is 4.9 lengths per second (less in trained swimmers; Fitts *et al.* 1989), and it seems likely that knee extensor muscles would be about equally fast. I have no data for bushbaby muscle, but bushbabies are similar in mass to rats in which a fast leg muscle (extensor digitorum longus) has a maximum shortening speed of about 15 lengths per second (Woledge *et al.* 1985). These data give shortening speed parameters ($8.4\dot{\epsilon}(s/g)^{\frac{1}{2}}$, see above) of nine for humans and ten for bushbabies. However, Tihanyi *et al.* (1982) give the maximum shortening speed of human knee muscles in terms of the angular velocity of the knee, as 18 rad per second for subjects with predominantly fast fibres. This is \dot{a}_{\max}/r_0 , implying that the shortening speed parameter is only $18 \times 0.21 = 4$. These data indicate that the parameter is likely to be in the range 4–10, for humans and bushbabies. Most of the graphs in this paper show data for a shortening speed parameter of 8, but the effects of variations in the range 2–32 have been investigated.

Orthopteran wing muscles have maximum shortening speeds up to 16 lengths per second (Josephson 1984). If locust knee extensor muscles were as fast as this, their shortening speed parameter would be $8.4 \times 16 \times 0.05 = 7$, about the same as for humans and bushbabies. The shortening speed seems actually to be much lower than this, about 1.8 lengths per second (Bennet-Clark 1975), giving a shortening speed parameter of only 0.8. It seems probable that the parameter is also small for smaller insects. For a flea, segment length s , would be of the order of 1 mm, making $(s/g)^{\frac{1}{2}}$ about 0.01 s. The fastest muscles that have been investigated have shortening speeds of about 25 lengths per second (Woledge *et al.* 1985). Even with muscles as fast as this, the shortening speed parameter of a flea would be only $8.4 \times 10 \times 0.01 = 1.7$. For some of the insect simulations, the parameter will be given a value of 1.

We must take account of the force the muscle can exert, in selecting values for series compliance. Sarcomeres are stretched about 1.5% by their isometric force (Huxley & Simmons 1971). Thus the lowest likely value for the series compliance of a muscle of length $8.4 r_0$ (see above) is $0.015 \times 8.4 r_0 / F_{m,iso} =$

$0.13 r_0 / F_{m,iso}$. At the other extreme, we may imagine a muscle whose tendon stretched elastically by $2.1 r_0$ (our estimate of the muscle's working range of length) when the muscle exerted its isometric force. In that case the compliance would be $2.1 r_0 / F_{m,iso}$. Results will be presented for compliance parameters $CF_{m,iso}/r_0$ ranging from 0.125 to 2.

The strain energy stored by elastic structures prior to the jump in locusts exceeds the energy of the jump, implying that the compliance parameter is a little more than 2 (Bennet-Clark 1975). Realistic values for mammals are harder to estimate. Isometric muscle forces impose stresses around 50 MPa on highly-stressed tendons such as the human gastrocnemius (Ker *et al.* 1988), stretching them by about 4% of their length (see figure 1.6 in Alexander 1988). Suppose that the total length of tendon or aponeurosis in series with each muscle fascicle is twice the length of the fascicle, a value within the commonly found range for pennate muscles. Then if the length of the fascicles is $8.4 r_0$ (as already estimated) the extension of the tendon is $2 \times 8.4 \times 0.04 r_0 = 0.7 r_0$ and the compliance parameter is 0.7.

5. RESULTS AND INTERPRETATION

This section presents results and tries to explain in words why the mathematical models behave as they do. Discussion of the light thrown by the models on the design and jumping techniques of real animals is deferred to the next section.

(a) Predicted forces

Figure 2 shows sample simulations, one for each of the three jumping techniques. The chosen isometric force ($1.0 mg s / r_0$) gives peak ground forces in the range 2–3 mg which is typical of human jumping.

Figure 2a shows a squat jump. Initially, the force on the ground equals body mass and the muscle is inactive. At time, $t = 0$, the muscle is activated and its contractile element starts to shorten, stretching the series elastic element and building up tension. By $t = 0.14(s/g)^{\frac{1}{2}}$ it is exerting enough moment to start extending the knee. The muscle force continues to rise as the series elastic elements are stretched further: but never reaches the isometric value because the contractile elements are shortening throughout take-off. Later, the muscle force falls because the contractile elements' rate of shortening is increasing, allowing the series elastic elements to recoil. Eventually, the muscle is exerting too little moment to maintain the angular acceleration of the leg segments that would be needed to keep the feet on the ground while the trunk continues to rise. The feet leave the ground at a knee angle (in this simulation) of 146°.

Figure 2b represents a catapult jump. In this case the muscle is active from the start, exerting its isometric force, and the series elastic element is correspondingly stretched. The knee is prevented from extending until $t = 0$, when it is suddenly released. The force on the ground rises abruptly and the body accelerates to take-off. As the knee extends, the series elastic elements

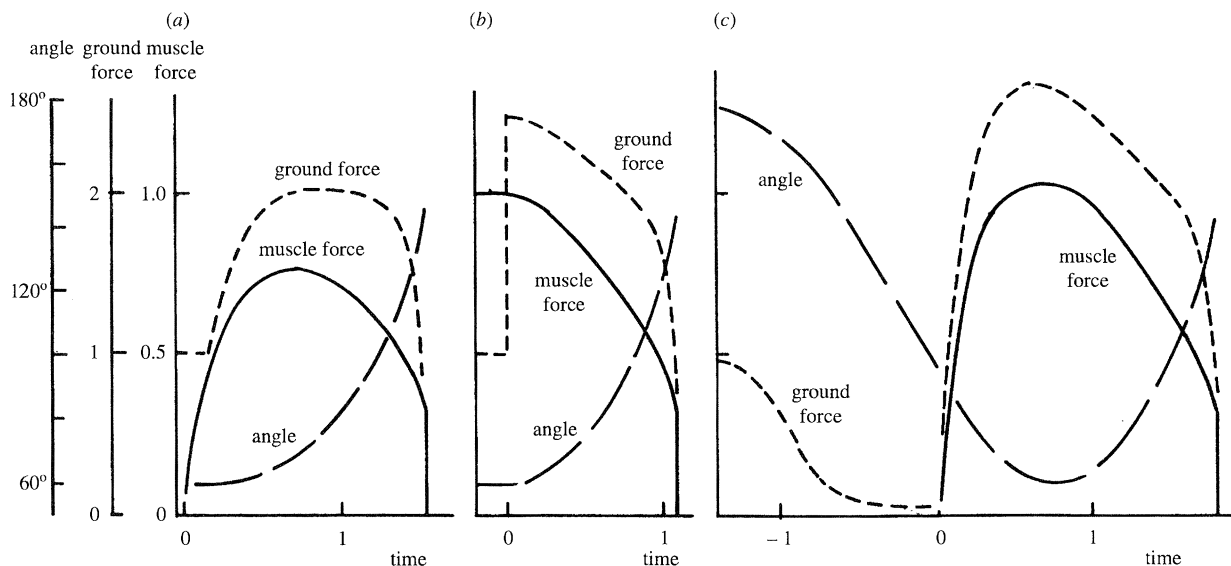


Figure 2. Examples of simulated jumps: (a) represents a squat jump; (b) a catapult jump; and (c) a countermovement jump. The force exerted on the ground (expressed as F_g/mg), the force exerted by the knee extensor muscles (expressed as $F_m/F_{m,iso}$) and the knee angle (2θ) are plotted against the time parameter $t(g/s)^{0.5}$. These are jumps by the model with two-segment legs (see figure 1a) with muscles exerting human-like forces (isometric force parameter $\hat{F}_{m,iso} = 1.0$). The shortening speed parameter \hat{a}_{max} is 8, the compliance parameter \hat{C} is 1.0 and segment masses are $m_1 = 0.7m$, $m_2 = 0.2m$, $m_3 = 0.1m$.

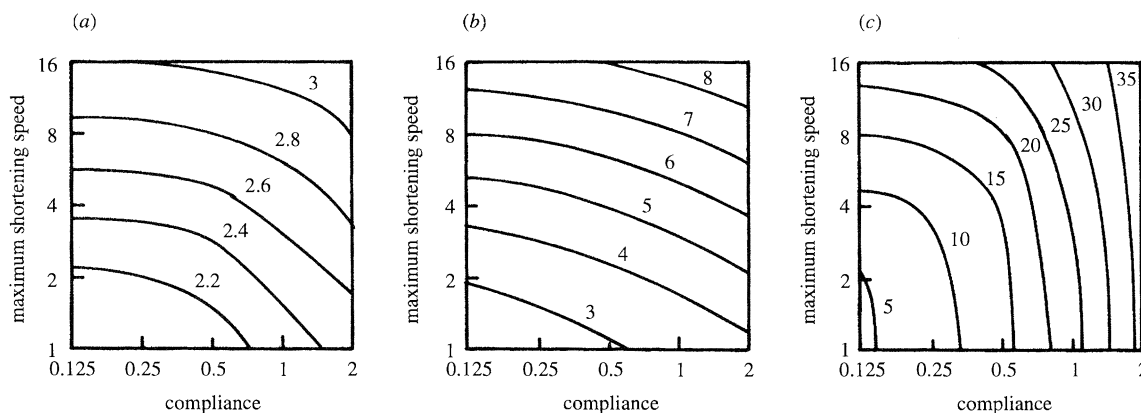


Figure 3. Contour plots showing the dependence of jump height on the maximum shortening speed of the muscles and their series compliance: (a) refers to countermovement jumps with human-like forces (isometric force parameter $\hat{F}_{m,iso} = 1$); (b) to countermovement jumps with bushbaby-like forces ($\hat{F}_{m,iso} = 5$); and (c) to catapult jumps with insect-like forces ($\hat{F}_{m,iso} = 25$). The axes show the shortening speed parameter \hat{a}_{max} and the compliance parameter \hat{C} , and the contours give relative jump height h/s . The legs have two segments, and segment masses are $m_1 = 0.7m$, $m_2 = 0.2m$ and $m_3 = 0.1m$, throughout.

recoil, the contractile elements shorten progressively faster and the muscle force falls.

Figure 2c represents a countermovement jump. Initially the leg is straight; the muscles are inactive but the feet rest on the ground exerting a force which diminishes as the body falls under gravity. The leg bends until, at $t = 0$ (when the knee angle, in this example, is 96°), the muscles are activated. Tension builds up and the fall is decelerated until at $t = 0.8(s/g)^{1/2}$ (in this example), when the knee angle is 60° , the fall is halted and the body begins to rise again. Immediately prior to this the muscle was being stretched and the force in it had risen a little above the isometric value (to $1.08F_{m,iso}$). In the very early stages of knee extension, the force is still above the isometric value: the contractile elements are still being stretched but the series elastic elements are shortening faster (by

elastic recoil) and the muscle, as a whole, is shortening – extending the knee. Only when the elastic recoil has proceeded far enough for the muscle force to drop below $F_{m,iso}$ do the contractile elements begin to shorten.

(b) *Effects of muscle properties*

Figure 3 shows how the height of a jump depends on the maximum shortening speed of the muscles and the series compliance: (a) for human-like ground forces; (b) for bushbaby-like ground forces; and (c) for insect-like ground forces. The simulations are of countermovement jumps in figure 3a, b and a catapult jump in figure 3c, in accordance with the jumping techniques used by humans, bushbabies and insects, respectively.

Comparison of figure 3a and 3b shows, as expected,

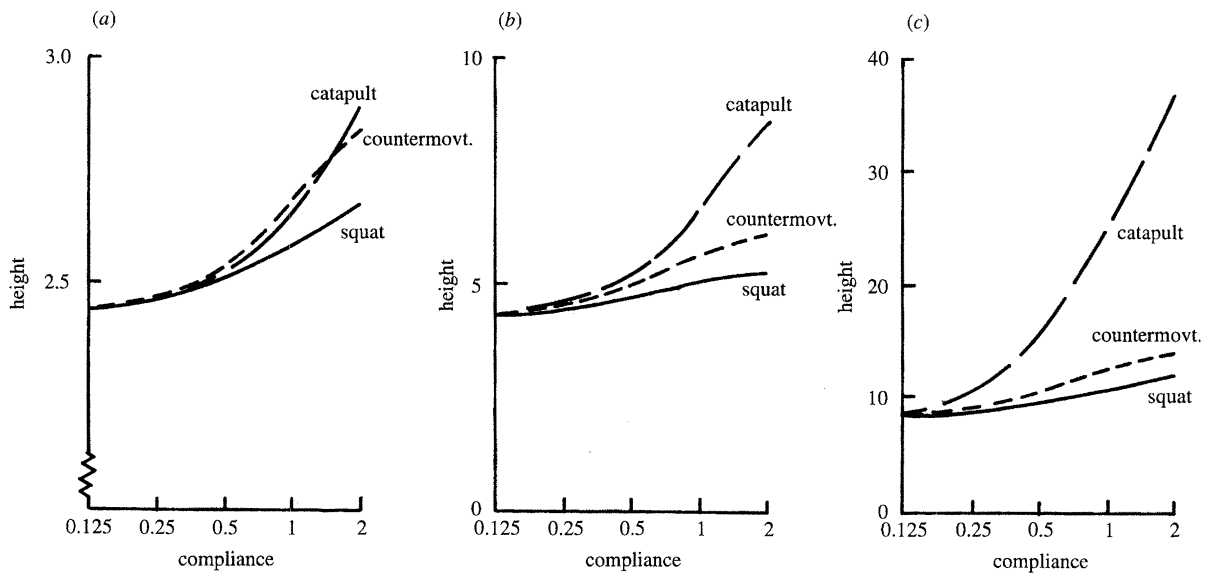


Figure 4. A comparison of three jumping techniques. In each graph relative jump height h/s is plotted against the compliance parameter \hat{C} , for: (continuous line) squat jumps; (short dashes) countermovement jumps; and (long dashes) catapult jumps. Isometric forces are (a), human-like ($\hat{F}_{m,iso} = 1$); (b), bushbaby-like ($\hat{F}_{m,iso} = 5$); and (c), insect-like ($\hat{F}_{m,iso} = 25$). In every case the shortening speed parameter \hat{a}_{max} is 8 and segment masses are $m_1 = 0.7m$; $m_2 = 0.2m$; and $m_3 = 0.1m$. The legs have two segments.

that larger muscle forces give higher jumps. Both these graphs refer to countermovement jumps, but isometric force (expressed as a multiple of body mass) is larger in *b* than in *a*, and jump heights (as multiples of leg length) are also larger. Examination of the contours on each graph shows that for constant isometric force, faster muscles and higher compliances given higher jumps. Faster muscles can exert more force, at given rates of shortening. Series elastic elements can shorten by elastic recoil at unlimited rates. Also, series elastic elements make it possible for muscle forces that are greater than the isometric force, developed during a countermovement, to persist into the early stages of leg extension. This was explained in §5*a*.

By how much might increased compliance be expected to improve jump height? In many cases, the peak force exerted by the muscles during takeoff is close to their isometric force $F_{m,iso}$ (see figure 2). This force, acting on compliance C , stores strain energy $\frac{1}{2}F_{m,iso}^2 C$ in each leg, a total of $F_{m,iso}^2 C$. By equations (26) and (28) this equals $\hat{F}_{m,iso} \hat{C} m g s$, enough to raise the animal's centre of mass by $\hat{F}_{m,iso} \hat{C} s$. Thus if all the stored strain energy were converted to gravitational potential energy in the jump, an increase in \hat{C} from 0.125 to 2 (the range investigated in figure 3) would improve jump height by 1.9*s* when $\hat{F}_{m,iso} = 1$; by 9.4*s* when $\hat{F}_{m,iso} = 5$; and by 47*s* when $\hat{F}_{m,iso} = 25$. The improvements predicted by the model are substantially less than this, as can be seen by comparing jump heights for compliance parameters of 0.125 and 2, for any chosen value of the shortening speed parameter, in figure 3*a, b* or *c*. Reasons for this include peak forces being less than isometric for squat jumps (see figure 2*a*) and some countermovement jumps; and to some energy being required to give kinetic energy to the legs (see §5*d*).

In countermovement jumps (see figure 3*a, b*) jump height is more sensitive to the speed of the muscles than

to the series compliance: an increase of (say) 10% in muscle shortening speed generally increases jump height more than a 10% increase in compliance. In catapult jumps (see figure 3*c*), however, jump height is more sensitive to compliance than to the speed of the muscles, except when compliance is very low.

The catapult jumps of figure 3*c* involve much larger isometric forces (relative to body mass) than do the countermovement jumps of figures 3*a, b*. The statements of the previous paragraph nevertheless remain true, when comparisons are made between countermovement and catapult jumps with equal isometric forces.

(c) Comparison of jumping techniques

Figure 4 shows results of simulations of the three jumping techniques, with the isometric muscle forces chosen to represent: (a) human jumping; (b) bushbaby jumping; and (c) insect jumping. Results are shown in each case for a range of series compliances, for one maximum shortening speed.

With zero series compliance, the three techniques would give jumps of identical height for the following reasons. In a squat jump, muscle force would rise instantaneously to the isometric value when the muscle was activated; and in a countermovement jump, muscle force would fall to the isometric value at the instant when the knee ceased bending and started to extend. Thus knee extension would start in every case with $\theta = \theta_{min}$, $\dot{a} = 0$ and $F_m = F_{m,iso}$.

As compliance increases, all three techniques give higher jumps but squat jumping is less successful than the others because muscle force is less than the isometric value when knee extension starts. The relative merits of catapult and countermovement jumping depend on the isometric force. In the human simulations the two techniques give similar jump heights (see figure 4*a*).

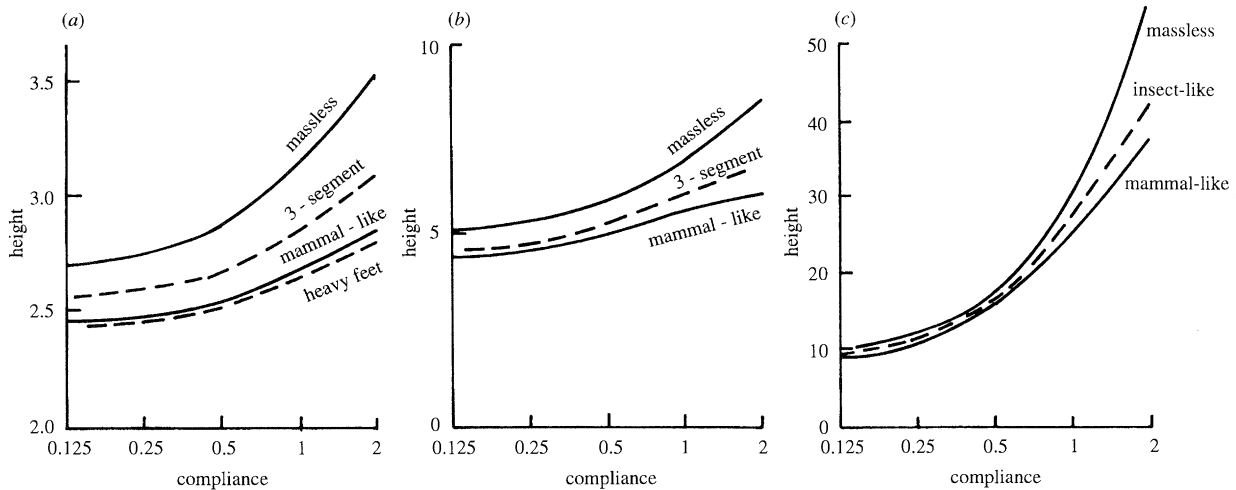


Figure 5. The effects on jump height of the mass and structure of the legs. Relative jump height h/s is plotted against the compliance parameter \hat{C} . Mass distributions are: massless legs: $m_1 = m$, $m_2 = 0$, $m_3 = 0$; insect-like legs: $m_1 = 0.83m$, $m_2 = 0.14m$, $m_3 = 0.03m$; mammal-like legs and 3-segment legs $m_1 = 0.7m$, $m_2 = 0.2m$, $m_3 = 0.1m$; heavy feet $m_1 = 0.7m$, $m_2 = 0.1m$, $m_3 = 0.2m$. Three segment legs are as shown in figure 1*b*; others as in figure 1*a*. (a) shows the heights of countermovement jumps with human-like forces ($\hat{F}_{m,iso} = 1$); (b), countermovement jumps with bushbaby-like forces ($\hat{F}_{m,iso} = 5$); and (c), catapult jumps with insect-like forces ($\hat{F}_{m,iso} = 25$). The shortening speed parameter \hat{a}_{max} is 8 in all cases.

With moderate compliances, countermovement jumps are a little higher than catapult jumps because the maximum muscle forces are greater than isometric (see figure 2*c*). If the compliance is very high, however, the potential energy lost in the body's fall in a countermovement is not enough to build up so much force in the series elastic elements, and catapult jumps are higher.

In the bushbaby and insect simulations (see figure 4*b, c*), isometric muscle force is not attained in countermovement jumps except when the series compliance is very low. Consequently, catapult jumps are higher than countermovement jumps over a wide range of compliances. In the insect case (see figure 4*c*) a countermovement gives very little advantage over a squat jump.

A simple calculation will give a rough indication of the circumstances in which a countermovement jump can be expected to be higher than a catapult jump. In simulations like those of figure 4, in which the minimum knee angle is 60° , the trunk falls a distance s in a countermovement which starts with the legs straight. The leg segments fall smaller distances, so the potential energy lost in the fall is a little less than mgs . When a muscle is exerting its isometric force, strain energy $\frac{1}{2}CF_{m,iso}^2$ is stored in its series elastic element. For the potential energy lost to supply enough strain energy to raise the force in the series elastic elements of both muscles to $F_{m,iso}$

$$mgs > CF_{m,iso}^2$$

$$\hat{C} < 1/\hat{F}_{m,iso}. \quad (29)$$

The right-hand side of this inequality is 1.0, 0.2 and 0.04 for the human, bushbaby and insect simulations, respectively. These are the maximum values of the compliance parameter \hat{C} at which countermovement jumps might be expected to be higher than catapult jumps. However, it should be noted that some of the strain energy may be supplied as work done by the

muscles, especially if the maximum shortening speed is high.

(d) Mass distribution in the legs

Figure 5 compares jumps by animals with different distributions of mass in their legs. As in previous figures, the isometric forces have been chosen to represent: (a) humans; (b) bushbabies; and (c) insects.

In each case, the highest jumps were achieved when the legs were given no mass. Mass in the legs reduces the height of the jump because some of the work done by the muscles is required to provide internal kinetic energy (energy associated with movement of parts of the body relative to the centre of mass). Unlike the external kinetic energy (associated with movement of the centre of mass), this energy does not become potential energy as the animal rises to the peak of the jump, so does not contribute to the jump's height. Some of the internal kinetic energy is associated with differences in the vertical component of velocity at take-off, between the leg segments and the trunk (see discussion of the effect of foot mass on jumping, Alexander 1988). The rest is due to the horizontal components of velocity given to parts of the legs, as the legs straighten in take-off.

The total mass of the legs seems more important than the distribution of mass within the legs. A mammal-like mass distribution, with the thighs twice as heavy as the lower leg ('mammal-like', figure 5*a*) gives only slightly higher jumps than when the masses of thighs and lower legs are reversed ('heavy feet'). This seems to be due to the part of the internal kinetic energy at take-off due to transverse components of velocity being larger than the part due to differences in vertical velocity. The former part is the same for both mass distributions (for given trunk velocity) but the latter part is greater when the lower leg is the heavier segment.

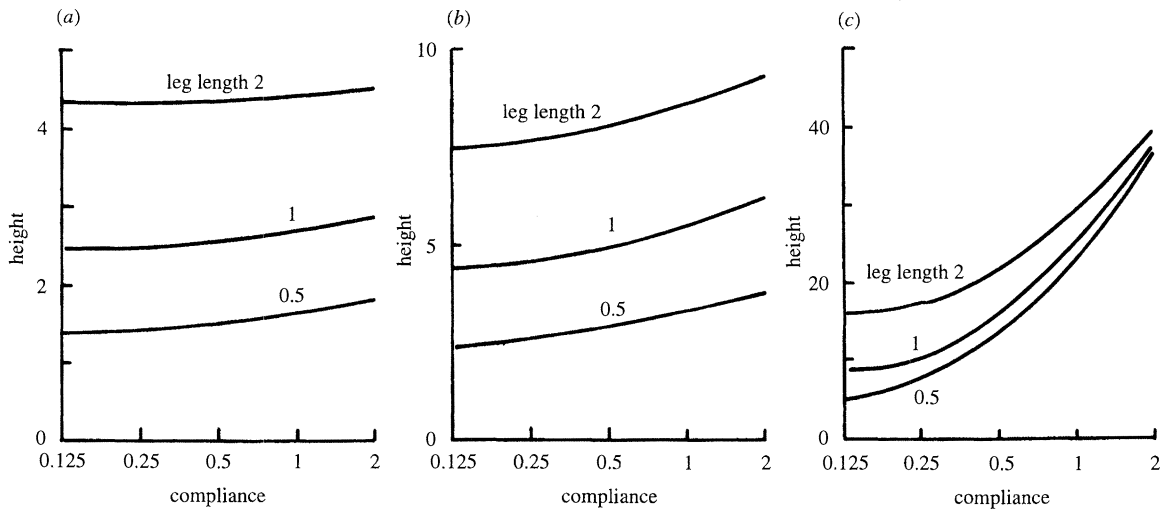


Figure 6. The effect of leg length on jump height. In each graph, relative jump height h/s , is plotted against the compliance parameter \hat{C} for three different relative leg lengths s'/s : (a) refers to countermovement jumps with human-like forces ($\hat{F}_{m,iso} = 1$); (b) to countermovement jumps with bushbaby-like forces ($\hat{F}_{m,iso} = 5$); and (c) to catapult jumps with insect-like forces ($\hat{F}_{m,iso} = 25$). Other details are as in figure 4, and as explained in the text.

The leg segments of jumping insects such as locusts are much smaller fractions of body mass than are those of humans and bushbabies (see §4). Figure 5c shows that even their mass reduces jump height appreciably, in comparison with hypothetical massless legs.

(e) Number of joints

Figure 5a, b also shows results for a model with three-segment legs (figure 1b). This jumps higher than the mammal-like two-segment model although it has the same distribution of mass along the legs. The reason is that the joints of the three-segment leg are initially closer to the vertical line through the hip. Therefore, the transverse displacements and transverse velocities that occur, as the leg straightens, are smaller for the three-segment leg. It was shown in the derivation of equation (20) that at the same vertical velocity y , the kinetic energy associated with transverse leg movement is only one quarter as much for three-segment legs, as for two-segment legs.

(f) Leg Length

To discover the effect of changing leg length we will compare animals with equal masses of leg muscle: that implies those with equal values of $F_{m,iso} r_o$, as $F_{m,iso}$ is proportional to the cross-sectional area of the muscle and (as explained in §4) r_o can be expected to be proportional to muscle fibre length. The leg muscles, of the animals to be compared, will be capable of shortening at equal numbers of lengths per second: hence, as explained in §4, they have equal values of \hat{a}_{max}/r_o . Thus we will compare a standard animal with leg segments of length s , with an isometric force parameter $\hat{F}_{m,iso}$ and a shortening speed parameter \hat{a}_{max} ; with a modified animal with legs of length s' , with an isometric force parameter $\hat{F}_{m,iso}(s/s')$ and a shortening speed parameter $\hat{a}_{max}(s'/s)^{3/2}$ (see equations (26) and (27)). The compliance parameter (see equation (28)) is not affected by the change of leg length. Jump

height will be expressed as a multiple of the standard leg length (i.e. as h/s). Because leg muscles are generally more massive than the leg skeleton, we will ignore any increase of leg skeleton mass that may be made necessary by increased leg length.

Results are shown in figure 6, calculated for isometric forces representing: (a) humans; (b) bushbabies; and (c) insects. In every case, longer legs give higher jumps. This is partly because longer-legged animals start a jump with the centre of mass higher above the ground. When the feet are on the ground with the knees bent at 60° (the starting angle in every case, in figure 6) the hips and centre of mass are a height $1.0s$ above the ground when relative leg length s'/s is 1.0, but $2.0s$ above the ground when $s'/s = 2.0$. In addition, longer legs enable the animal to accelerate over a greater distance, so the muscles do not have to shorten in so short a time, to accelerate the animal to given speed. Their rate of shortening can be lower so they can exert more force (see figure 1c) and do more work.

Notice that for catapult jumps simulating those of insects (figure 6c), leg length has little effect on jump height when compliance is high. The reasons are that jump heights are large multiples of leg length, so the initial height of the centre of mass from the ground is relatively unimportant; and the work done by elastic recoil is the same, whether the recoil is fast or slow.

(g) Moment arms

Suppose a given volume of muscle of given properties is required to operate a joint. Anatomical considerations may make it convenient to have a long-fibred muscle with a large moment arm, or a short-fibred muscle with a short moment arm. But if fibre length is made proportional to moment arm, these two muscle arrangements will have precisely the same mechanical effect: they can exert the same moment and move the joint at the same angular velocity (Alexander 1981). Because muscle volume is assumed constant, longer fibres imply a smaller physiological cross-sectional

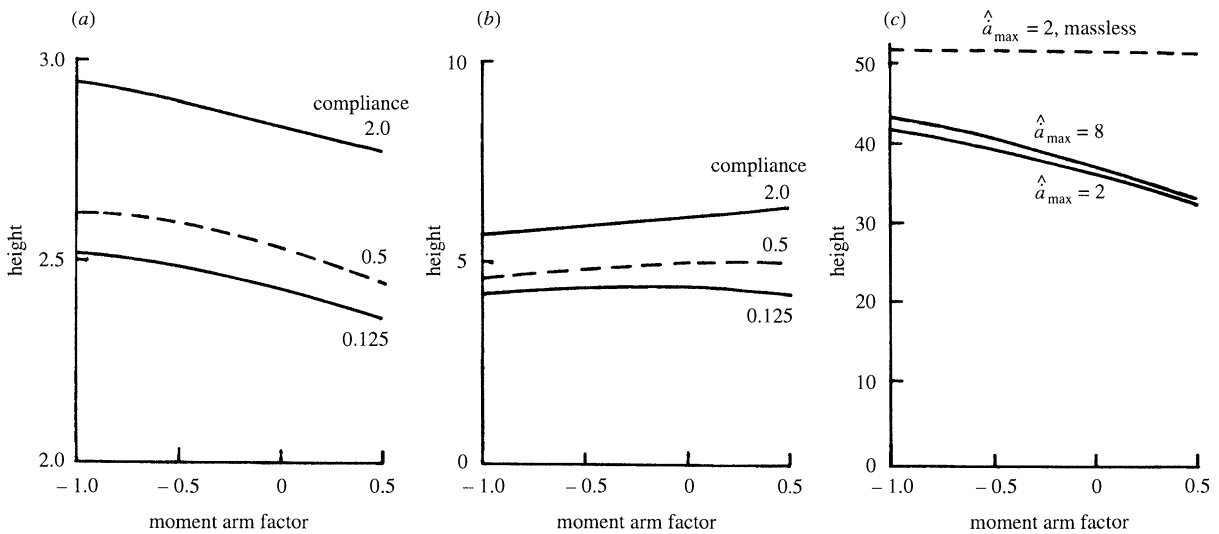


Figure 7. The effect of changing moment arms on jump height. Relative jump height h/s is plotted against the moment arm parameter k (equation 24): (a) shows the heights of counter-movement jumps with human-like forces ($\hat{F}_{m,iso} = 1$) for three different values of the compliance parameter \hat{C} ; (b) shows the heights of counter-movement jumps with bushbaby-like forces ($\hat{F}_{m,iso} = 5$), for the same three values of the compliance parameter; and (c) shows the heights of catapult jumps with insect-like forces ($\hat{F}_{m,iso} = 25$) for two values of the shortening speed parameter. In (a) and (b) the shortening speed parameter is 8. In (c) the compliance parameter is 2. The legs have two segments. Segment mass are $m_1 = 0.7m$, $m_2 = 0.2m$, $m_3 = 0.1m$ except in the case of the broken line in (c), for which $m_1 = m$, $m_2 = m_3 = 0$.

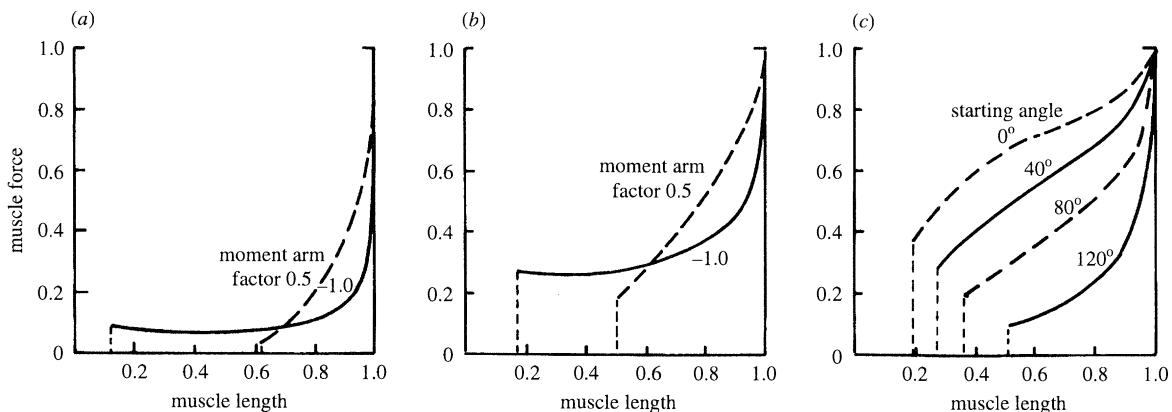


Figure 8. Graphs of muscle force ($F_m/F_{m,iso}$) against muscle length, for selected jumps with muscles of zero compliance. Muscle length is expressed as a fraction of the working range, so that it is zero when the leg is fully extended and 1.0 when the knee is bent to its minimum angle. (a) and (b) compare jumps with different moment arm factors k , for jumps with bushbaby-like forces ($\hat{F}_{m,iso} = 5$) and (a) slow muscles, $\hat{a}_{max} = 4$ and (b) fast muscles $\hat{a}_{max} = 16$. (c) compares jumps with different starting angles $2\theta_{min}$ for jumps with human-like forces ($F_{m,iso} = 1$) and a shortening speed parameter of 8. All graphs refer to two-segment legs with $m_1 = 0.7m$, $m_2 = 0.2m$, $m_3 = 0.1m$.

area. For this reason, we will not investigate the effect of changing the mean moment arm r_o .

There may, however, be an advantage in having a moment arm that changes, as the joint extends. This is achieved in the models by giving the factor k (equation (24)) a non-zero value. When k is positive the moment arm increases as the joint extends. The mean moment arm, over the range of knee angles from 60° to 180° , equals r_o for all values of k .

Figure 7a shows that for counter-movement jumps with isometric forces representative of humans, the lowest values of k give the highest jumps. Figure 7c shows that the same is true of catapult jumps with insect-like forces. Figure 7b, however, shows that for counter-movement jumps with bushbaby-like ground forces, the highest jumps may be obtained with the highest values of k (for the higher compliances in this

figure) or with intermediate values (for low compliances). In these simulations, the muscles were given a maximum shortening speed which is believed to be realistic for small mammals such as bushbabies (see §4). Simulations with faster muscles gave the highest jumps for the lowest values of k , as in figure 7a.

To explain these confusing results we must consider both the force-velocity properties of the muscles and the influence of leg mass. To see the effects of the force-velocity properties clearly, we will compare jumps with zero series compliance. As already explained (see §5c) such jumps are identical whether a squat, catapult or counter-movement technique is used. In figure 8a, b, muscle force is plotted against muscle length for jumps with different values of k . In all cases, the muscle initially exerts its isometric force, but the force falls as the muscle shortens at an increasing rate.

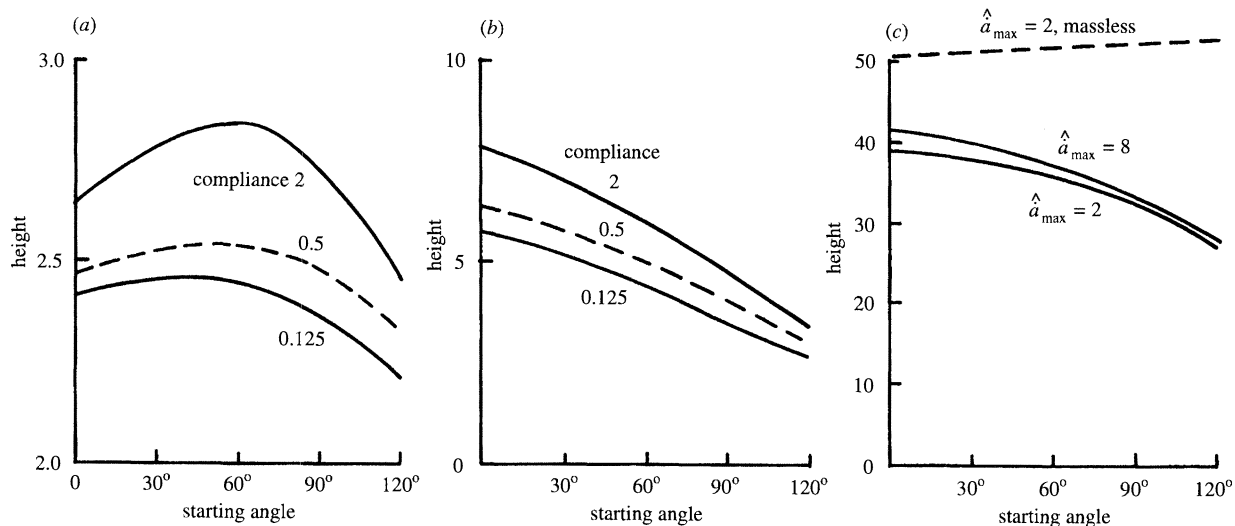


Figure 9. The effects of starting angle on jump height, when the muscles are adapted to the starting angle as explained in the text. Relative jump height h/s is plotted against starting angle $2\theta_{\min}$ for countermovement jumps with: (a) human-like; (b) bushbaby-like forces; and (c) catapult jumps with insect-like forces. Other details are as for figure 7.

At first it falls faster for negative values of k . This is because negative values of k give moment arms which are initially high, requiring the muscle to shorten faster for any given angular velocity of the joint. Later, however, muscle force falls more slowly for negative values of k (for which the moment arm is decreasing) than for positive values (for which it is increasing). Consequently, the graphs for negative and positive values of k cross, and the negative values give the higher muscle forces in the later stages of take-off.

The areas under the graphs in figure 8 represent the work done by the muscles. In figure 8a the maximum shortening speed of the muscle is low and the muscle does 8% less work for $k = -1$ than for $k = +0.5$. In figure 8b however, a faster muscle does 18% more work for $k = -1$ than for $k = +0.5$. These simulations used bushbaby-like muscle forces, as did the simulations in figure 6b in which the maximum shortening speed of the muscles has an intermediate value.

The optimum value of k in countermovement jumps depends mainly on the force-velocity properties of the muscles, though series compliance also has an effect, as figure 7b shows. The heights of catapult jumps with insect-like muscle forces and high series compliances depend very little on the force-velocity properties of the muscles (see figure 3c), and in such cases we must look for a different explanation of the dependence of jump height on k .

An explanation is suggested by a comparison in figure 7c, between the continuous lines (for legs with mass) and the broken one (for legs of zero mass). The former show lower jump heights for the reason given in §5d; some of the work done by the muscles is required to provide internal kinetic energy associated with movement of leg segments relative to the centre of mass. Another difference between the continuous and broken lines is that the former show jump height decreasing as k increases, but the latter shows heights that are almost independent of k . The reason that leg mass makes jump height dependent on k is that a major

part of the internal kinetic energy at take-off (represented by the term $m_4 \tan^2 \theta$, in equation (13)) is proportional to $\tan^2 \theta$ which approaches infinity as the leg straightens. Consequently, less work is needed to accelerate the body to a given speed if it reaches this speed while the legs are still considerably bent, than if it does not reach it until the legs are almost straight. A negative value of k makes the moment arm initially high, enabling the elastic recoil of the series compliance to do most of its work early in the process of leg extension.

(h) Joint angles

So far we have assumed that the minimum knee angle occurring in the jump ($2\theta_{\min}$) is 60° ; the working range, from this to full extension, is 120° . We will now ask whether there would be an advantage in working over a different range, for example from 0° to full extension (a range of 180°) or from 120° to full extension (a range of 60°). Assume that the volume of the muscle and the properties of its constituent fibres are constant. Then to adapt the muscle to work over a range of 180° (for example) instead of 120° , the length of its fascicles should be multiplied by 1.5 and their physiological cross-sectional area by 0.67. Its maximum shortening rate would then be 1.5 times, and its isometric force 0.67 times, the values for 120° range. More generally, if the range is to be multiplied by a factor n , \dot{a}_{\max} is multiplied by n and $F_{m,iso}$ is divided by n . Also, if the series elastic element is to be stretched by the same fraction of muscle fascicle length, when the muscle exerts its isometric force, the compliance C must be multiplied by n^2 .

These adjustments were made in the calculations for figure 9, which shows jump heights for different minimum knee angles. Jump height is greater for lower minimum knee angles except in figure 9a, which shows intermediate angles giving the highest jumps.

Figure 8c will help us to understand these results.

Like the other parts of this figure it shows muscle force plotted against length, for a muscle with no series compliance. The greater the minimum angle, the faster muscle stress falls as the body accelerates and the less work does the muscle do. (Remember that work is represented by the areas under the graphs.)

Our assumptions imply that the muscle has the same volume in every case and is, in principle, capable of performing the same amount of work in a contraction. However, when the minimum angle is larger, the distance over which the body has to be accelerated to take-off speed is less, so it has to be accelerated in less time to reach the same speed. Consequently, the muscles shorten faster and can exert less force, when the minimum angle is high.

The argument so far suggests that the lowest minimum angles should give the highest jumps. However, figure 9*a* shows that for jumps with human-like isometric forces a minimum angle of 40° gives a higher jump than does one of 0° . The muscles do 22% less work, but the resulting jump is higher. The explanation is that with a minimum angle of 0° the hips start at ground level, but if the angle is 40° they start at a height $2s \sin 40^\circ = 0.68s$.

This effect can only be significant if jump height is quite small, compared to leg length. The difference of starting height is too small to counteract the advantage of a very low minimum angle, in the simulations with bushbaby-like muscle forces (see figure 9*b*).

There is another advantage of low minimum angles which has limited importance in the simulations of mammal jumps but predominates in jumps with insect-like muscle forces (see figure 8*c*). This is that the lower the minimum angle, the more of the muscle's work can be done while the leg is still quite strongly bent, and the lower the proportion of this work that is lost as internal kinetic energy. The argument in §5*f*, relating to the term $m_4 \tan^2 \theta$ in equation (13), applies again here. Simulations with insect-like muscle forces and legs of zero mass give jump heights almost independent of minimum angle.

6. DISCUSSION

The models presented in this paper are highly simplified. Their anatomies resemble those of real animals only in broad outline. Many simplifying assumptions have been made: for example, that muscles are fully activated instantaneously and that, if there are several extensor muscles, they are activated simultaneously. These assumptions were avoided by Pandy *et al.* (1990) in an optimal control model of human jumping. There is much uncertainty about the values of muscle properties such as maximum shortening speed and series compliance, which would be realistic for any particular species. The results nevertheless may help us to understand the principles of jumping.

They show us that different jumping techniques are appropriate for animals exerting forces that are different multiples of body mass. As a general rule, larger animals exert forces that are smaller multiples of body weight (Alexander 1985): humans making

standing jumps exert forces on the ground of 2–3 times body weight, and fleas over 100 times body weight (see §4). However, frogs exert maximum forces of only about 3.5 times body weight (Hirano & Rome 1984). Despite the difference in size between them and humans, the maximum forces they exert are not much greater, relative to body weight.

Figure 4*a* tells us that with human-like muscle forces, countermovement and catapult jumps are higher than squat jumps. Humans use the countermovement technique and healthy young men jump about 5 cm higher with a countermovement than they can in a squat jump (Komi & Bosco 1978). For them, leg segment length s is about 45 cm, so the advantage in jump height that a countermovement gives is 0.1*s*. This matches the advantage given by the simulations for a compliance parameter of 1.0. It was argued in §4 (admittedly on sparse evidence) that a compliance parameter of 0.7 might be realistic for mammals.

Figure 4*b* shows that for animals exerting bushbaby-like forces, catapult jumps could be much higher than countermovement jumps, which in turn can be higher than squat jumps. Mammals seem not to have evolved catapult mechanisms, so the options available to them are countermovement jumping and squat jumping. The larger prosimians make a countermovement before jumping, as is shown by forces falling below body mass in records of jumps by *Lemur catta* (2.4 kg) and *Galago garnetti* (0.8 kg: see figure 6 of Günther *et al.* 1991). The small bushbaby *Galago moholi* sometimes makes a small hop which may function as a countermovement, before jumping (Günther *et al.* 1991).

Figure 4*c* shows that catapult jumping is by far the most effective jumping technique for animals exerting insect-like ground forces. A variety of catapults have evolved in insects including the resilin springs of fleas (Bennet-Clark & Lucey 1967) and the apodemes and semilunar processes of locusts (Bennet-Clark 1975). The compliances of these catapults are high, enough in the locust for their elastic recoil to move the knee through its whole angular range (Bennet-Clark 1975). Figure 3*c* shows that for catapult jumps with such high compliances, the maximum shortening speed of the muscle makes little difference to the height of the jump. The knee extensor muscles of locusts seem to be slow, with maximum shortening speeds of only 2 lengths per second (Bennet-Clark 1975). It is probably inevitable that they should be fairly slow, as their sarcomeres are long, with 5.5 μm -thick filaments. They exert high isometric stresses, of about 0.7 MPa. Muscles with long thick filaments can exert high stresses because large numbers of cross-bridges connect each thick filament to a neighbouring thin one, but they tend to be slow because high cross-bridge cycling rates are needed to make the muscle contract at any given strain rate (Ruëgg 1968). The long sarcomeres of locust knee extensor muscle allow it to exert high stresses, enabling a given volume of muscle to do a large quantity of work as it shortens to deform the catapult springs. The good effect of this on jump performance must far outweigh the small disadvantage of the muscles' being slow.

Figure 5 shows that jump height is reduced by heavy legs. However, if the jump is powered by a leg muscle

(as in locusts) that muscle must be large to power a strong jump, and the leg cannot be very light. Comparison of the simulations with mammal-like leg proportions in figure 5*a* with those with thigh and lower leg masses reversed shows that the total mass of the leg influences jumping ability more than the distribution of the mass. This is in contrast to running, for which it is particularly important that the distal parts of the limbs should be light, to minimize the kinetic energy required for each forward or backward leg swing (Fedak *et al.* 1982). Jumping vertebrates do not have the very light feet found in unguulates.

The finding that legs with more than two segments make higher jumps possible is striking (see figure 5*a, b*). It seems to throw light on the evolution of the elongated tarsal bones of bushbabies and frogs (illustrated in Rogers 1986) which, in effect, add a segment to the lower leg. The long ilia of frogs, with their moveable iliosacral joints, add a further functional segment to frog legs.

When humans jump, the forefoot presses on the ground and the heel rises off the ground, so the metatarsals form an additional short leg segment. The importance of this was stressed by Bobbert & van Ingen Schenau (1988).

Figure 6 shows that longer legs can be expected to make higher jumps possible. Accordingly, many jumping vertebrates have longer legs than related animals of similar mass, that do not jump (Emerson 1985). Figure 6*c* suggests that for small insects using catapult mechanisms, the advantage of long legs might be small. Locusts have remarkably long hind legs but (as Dr R. F. Ker has pointed out to me) flea beetles (*Phyllotreta*) do not.

Figure 7*a, c* indicates that, to be most effective for jumping, the moment arms of the knee extensor muscles of humans and insects should decrease as the joint extends. The reverse is found both in humans and in locusts. The kinematics of the human knee is complicated by the effect of the patella (Bishop 1977), but Lindahl & Movin's (1967) graphs of quadriceps elongation against knee angle show that the muscles' effective moment arm is 80% greater when the knee is near full extension than when it is bent to 90°. The explanation here may be that the leg is principally adapted for walking and running, in which maximum forces act when the knee is much straighter than when bent in preparation for a jump.

The moment arm about the knee of the extensor tibiae muscle of locusts is very small when the knee is fully flexed and increases as the knee extends (Bennet-Clark 1975). This is an essential feature of the catapult mechanism because it enables the small flexor tibiae muscle to hold the knee flexed while tension builds up in the extensor. The requirements of the catapult release mechanism apparently override the advantage (indicated by figure 7*c*) of a moment arm that decreases as the joint extends.

Lutz & Rome (1994) found that the semimembranosus muscles of frogs shorten at a constant rate during take-off for a jump, presumably a consequence of moment arms that fall as the leg extends.

Figure 9 suggests that humans should not bend their

legs as much as bushbabies and insects, when preparing to jump. This is observed; humans bend the knee to about 75° (Bobbert & van Ingen Schenau 1988), *Galago* to 30° (Günther 1985) and locusts almost to 0° (Heitler 1977). I am not inclined to attach much significance to this correspondence between theory and observation because human legs are not principally adapted for jumping.

Jumping is a relatively simple process, performed in similar ways by a wide variety of animals. An objective (to jump as high or as far as possible) is easily defined. These features make jumping a peculiarly attractive subject for investigations such as this one, which has explored the effects of muscle properties, leg design and technique on jumping performance.

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