

JUMPING PERFORMANCE OF HYLID FROGS MEASURED WITH HIGH-SPEED CINE FILM

RICHARD L. MARSH AND HENRY B. JOHN-ALDER

*Department of Biology, Northeastern University, 360 Huntington Avenue, Boston,
MA 02115, USA and Department of Biological Sciences, Rutgers University,
Piscataway, NJ 08854, USA*

Accepted 8 November 1993

Summary

Jumping performance at 20 °C was assessed in five species of hylid frogs using high-speed cine film. Mean takeoff velocities (V_t) varied from 1.5 to 2.4 m s⁻¹ among the species. Peak V_t varied from 1.9 to 2.9 m s⁻¹. Body-mass-specific power output averaged over the entire takeoff period varied from 29 to 91 W kg⁻¹ during the jumps with the highest takeoff velocities. These values are similar to those predicted from jumping distance. As the mass of muscles available to power the jump probably amounts to no more than 17% of the body mass, average muscle-mass-specific power can be over 500 W kg⁻¹. The performance during jumping is even more impressive in view of the fact that the peak power during takeoff is about twice the average power. These frogs must use elastic storage to redistribute power during takeoff to produce the peak power required and may use pre-storage of elastic energy to boost the average power available.

Introduction

Jumping by anuran amphibians provides an excellent opportunity to evaluate the performance of skeletal muscle during natural movements, but this opportunity has remained largely unexploited (Marsh, 1994). Much is known about the performance of anuran muscle *in vitro* (e.g. Woledge *et al.* 1985), but many fewer studies have examined the detailed kinematics or dynamics of jumping in these animals (Hirsch, 1931; Calow and Alexander, 1973; Hirano and Rome, 1984). Fortunately, the relatively simple mechanics of jumping make it possible to circumvent somewhat this paucity of data by estimating work and power output from jumping distance. Considerable information is available on jumping distance (e.g. Emerson, 1978; Zug, 1978; John-Alder *et al.* 1988). Power output as estimated from jumping distances is high when examined in the context of values found for *in vitro* power output during isotonic contractions (Marsh, 1993).

Confirmation of these calculations based on jumping distance using kinematic or dynamic measurements would be worthwhile, but existing studies are not very helpful in this regard. Ground reaction forces during jumping by ranid frogs (Calow and Alexander,

Key words: jumping, power output, hylid frog, *Osteopilus septentrionalis*, *Hyla cinerea*, *Hyla squirella*, *Pseudacris crucifer*, *Acris gryllus*, takeoff velocity.

1973; Hirano and Rome, 1984) appear to have been recorded during submaximal jumps, as judged from measurements of jumping distance on the same or similar species. Several authors have reported data from filming studies of jumping (Hirsch, 1931; Gans, 1961; Calow and Alexander, 1973; Altevogt *et al.* 1986), but only Hirsch provides detailed calculations of force and acceleration that reveal the distribution of force and power during takeoff. However, his calculations (Hirsch, 1931) appear to be at odds with the force plate records of Calow and Alexander (1973). Hirsch calculates that acceleration (and thus force) is maximal early in the jump and then declines throughout takeoff, whereas Calow and Alexander (1973) found that ground reaction forces are low and variable at the onset of the jump, increase rapidly to a plateau, and then decline sharply just before takeoff. The fastest takeoff velocity (3.3 m s^{-1}) recorded by Altevogt *et al.* (1986) certainly appears to be compatible with the long jumping distances recorded in some other species, but a direct comparison of the kinematics of takeoff and jumping distance in the same species would be useful.

This present study examines jumping in several species of hylid tree frogs using high-speed cine films. We use data obtained from these films to calculate work and power output during jumping and compare these calculations with values based on jumping distance (John-Alder *et al.* 1988). An excellent record of a single jump by a Cuban tree frog (*Osteopilus septentrionalis*) also provided us with the opportunity to evaluate the distribution of power output during takeoff.

Materials and methods

Animals

The methods for collection and maintenance of the frogs used in this study were similar to those described by John-Alder *et al.* (1988). The animals were housed at a similar temperature (20–23 °C) to that used in the jumping trials.

Filming

Frogs were filmed in lateral view with a LoCam cine camera (Redlake Corp.) at a framing speed of approximately 300 Hz. Framing speeds for each segment of film analyzed were confirmed using timing marks recorded at 100 Hz on the edge of the film. The frogs were made to jump by moving a hand quickly towards them or lightly tapping their hind legs. We observed the takeoff and, in some jumps, the landing of the frog and estimated the angle of the jumping plane with reference to a plane parallel to the focal plane of the camera. The jumping surface was covered with rough-textured cloth to prevent slipping during takeoff. The air temperature near the jumping surface was regulated at 20 °C. The body temperature of the frogs measured just before jumping ranged from 19.5 to 20.0 °C.

Films were analyzed by projecting them with a Lafayette motion analyzer onto the surface of a HiPad Digitizer (Houston Instruments) connected to an Apple IIe microcomputer. The lowest resolution of the digitizing pad, which occurred when digitizing the largest frogs, was 0.15 mm of calibrated distance. If the frog jumps in a plane not strictly parallel to the focal plane of the camera, takeoff velocities could be

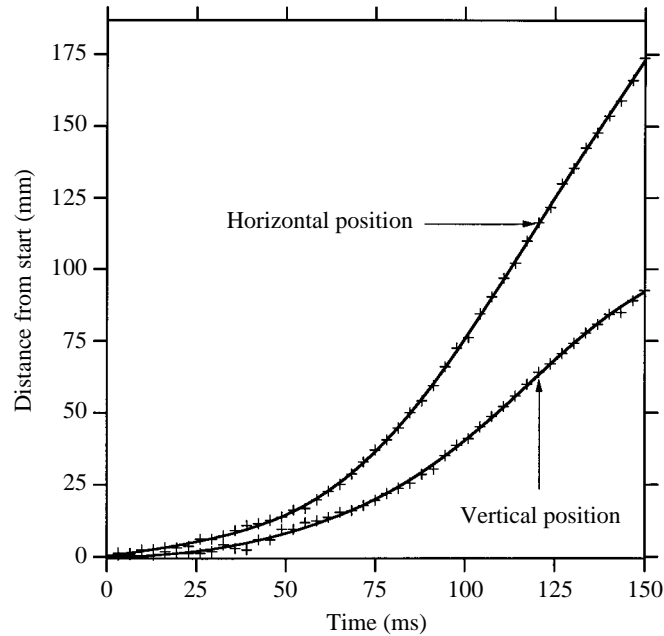


Fig. 1. Horizontal and vertical positions of the center of mass of an *Osteopilus septentrionalis* during the first part of a jump. The takeoff angle was 30° with a velocity of 2.5 m s^{-1} . The arrows indicate the point of takeoff, which occurred at 121 ms. The crosses are the points digitized from the a cine film with a framing speed of $306.5 \text{ frames s}^{-1}$. The smoothed curve is an eighth-order polynomial fitted to the data.

underestimated, as the projected distance moved will be less than the actual distance. These potential errors were minimized in two ways. First, we only used data from jumps in which the plane of the jump was less than 30° from the focal plane. Second, the total length of the frog from the nose to the tip of the toes with the hindlimbs fully extended was used as an internal length calibration on the films. Just after takeoff, the frog's body segments were completely aligned, and thus measurements of total length made on the individual frogs provided an accurate way to calibrate the apparent movements measured from the films. We measured the movement of the midpoint of the coccyx (urostyle), which represents the approximate center of mass (see below). However, at takeoff, there was little rotation of the trunk in most jumps and any point on the trunk or head would have sufficed to measure takeoff velocity. Takeoff velocity was estimated by averaging the change in distance for five frames centered on the frame in which takeoff occurred. The change in velocity is minimal over this time period (Fig. 1), and averaging considerably reduced the errors inherent in differentiating position data. We estimated the height of the center of mass at takeoff by estimating the horizontal position of the center of mass and measuring the height using a length scale painted on the takeoff surface at that horizontal position. Contact time was measured as the time from the first detectable movement until both feet left the ground. Takeoff angle was measured from the frame at takeoff and corrected geometrically for the deviation of the jumping plane from the focal

plane of the camera. Optimizing the field of view of the camera and the location of the jumping platform to measure the parameters of takeoff precluded measuring jumping distance in the same jumps.

For the single jump that we used to calculate force and power throughout the jump, we digitized the approximate center of mass from the first movement detected until shortly after takeoff. Careful measurements of the center of mass during jumping in *Rana ridibunda* by Hirsch (1931) indicated that in this species the center of mass lies near the center of the coccyx. The distribution of mass among body segments is similar in *Osteopilus* and *Rana ridibunda*. We therefore digitized the approximate center of the coccyx throughout the jump, this being our estimate of the center of mass. The center of mass is expected to move rearward slightly during the jump (Hirsch, 1931), but we ignored this effect. Hirsch (1931) estimated that this rearward movement amounted to about 3% of the length of the frog. Ignoring this movement of the center of mass would have the effect of slightly overestimating force and power early in the jump and underestimating these values later in the jump. The jump analyzed was almost exactly in the focal plane of the camera. Before takeoff, the x,y -coordinates digitized from the films were fitted with an eighth-order polynomial to provide a smoothed curve from which to calculate force and power. After takeoff, horizontal velocity was assumed to remain constant, and vertical velocity was assumed to decline, as determined by the acceleration due to gravity (Fig. 1).

Calculations

Calculating total work (W_j) and average power (\dot{W}_j) from the film records in the present study is straightforward, as takeoff velocity (V_t), height of the center of mass (H_t), and contact time (t_c) were all measured directly from the films. Body-mass-specific total work is the sum of the body-mass-specific kinetic (W_k) and potential (W_p) energies at takeoff, calculated as:

$$W_k = 0.5V_t^2 \quad (1)$$

and

$$W_p = gH_t, \quad (2)$$

where g is the acceleration due to gravity. Average power is, of course, total work divided by contact time.

Calculating work and power from jumping distance as reported in the literature is more complicated. First, the calculations require the assumption that the jumps were undertaken at the optimum takeoff angle (θ). However, the dependence on takeoff angle is not great, and this assumption introduces little error even if the frog deviates from the optimum angle by 10° (Gray, 1968; Marsh, 1993). Total jumping distance (L_j) can be subdivided into three components: (1) the forward distance traveled by the center of mass before takeoff ($L_{j,t}$); (2) the distance traveled between the time of takeoff and the time the center of mass descends below the level of takeoff ($L_{j,l}$); and (3) the distance traveled after the center of mass descends below takeoff height ($L_{j,d}$). Whether it is necessary to separate these components depends on the parameter to be calculated (Marsh, 1993). The total work done during takeoff is the sum of potential and kinetic energy components. However, both of these components contribute to jumping distance, and body-mass-

specific work can be estimated using the following equation that assumes that all of the energy is kinetic:

$$W_j = \frac{L_j g}{2 \sin 2\theta}, \quad (3)$$

where g is the acceleration due to gravity.

In contrast, calculating the average power expended (\dot{W}_j) requires that takeoff velocity (V_t) be estimated so that contact time (t_c) can be calculated. Takeoff velocity can be calculated from $L_{j,l}$ because this is the component of jumping distance that is determined by the kinetic energy at takeoff. The other components of jumping distance ($L_{j,t}$ and $L_{j,d}$) are related to the linear dimensions of the frog (Marsh, 1993) and their sum is almost constant if the frog fully extends its hindlimbs and takes off at near the optimal angle. Marsh (1993) suggested that, in the absence of direct data on $L_{j,l}$, this value can be estimated as:

$$L_{j,l} = L_j - 1.41 L_{cm}, \quad (4)$$

where L_{cm} is the distance from the tip of the toes to the center of mass at takeoff along the extended hindlimbs (Marsh, 1993). L_{cm} is approximately 1.15 times the hindlimb length (L_h). Takeoff velocity (V_t) is then calculated as:

$$V_t = \left(\frac{L_{j,l} g}{\sin 2\theta} \right)^{0.5}. \quad (5)$$

Contact time is:

$$t_c = \frac{2L_{cm}}{V_t} \quad (6)$$

(Marsh, 1993; see also equations 4 and 5 in Bennet-Clark, 1977). Finally, body-mass-specific average power is:

$$\dot{W}_j = \frac{W_j}{t_c}. \quad (7)$$

Results

We obtained usable films for 27 jumps by five species of frogs (Table 1). Takeoff angle averaged $40 \pm 4^\circ$, which is close to the optimum angle predicted for these frogs given their size and takeoff velocities (Marsh, 1993). The variable sample sizes reflect variability both in the responses to the test situation and in the number of animals available for testing. The most consistent performers in the tests were *Osteopilus septentrionalis*, the Cuban tree frog, and *Pseudacris crucifer*, the spring peeper. Peak takeoff velocities ranged from 1.9 to 2.9 m s^{-1} . Body-mass-specific work during peak efforts ranged from 2.3 to 4.6 J kg^{-1} . At takeoff, 10–20% of the work performed could be attributed to potential energy, with the higher values occurring in the species with the lower takeoff velocities. Body-mass-specific average power ranged from 30 to 90 W kg^{-1} . Comparable values for work and power at 20°C were estimated from the jumping distances recorded by John-Alder *et al.* (1988) (Table 2).

Table 1. *Jumping performance at 20 °C of five species of hylid tree frogs as measured in this study from high speed cine films*

Species*	N†	Mass (g)	L _{hl} (mm)	t _c (ms)		V _t (m s ⁻¹)	W _k (J kg ⁻¹)	W _p (J kg ⁻¹)	W _j (J kg ⁻¹)	Ẇ _j (W kg ⁻¹)
				Actual	Predicted‡					
Mean values										
<i>O. s.</i>	8 (2)	27.9	110	103±6	107±7	2.43±0.13	3.00±0.30	0.70±0.56	3.70±0.30	37.7±4.5
<i>H. c.</i>	4 (3)	8.7±0.1	71±0.2	90±3	97±4	1.69±0.07	1.45±0.12	0.50±0.03	1.94±0.14	22.4±2.6
<i>H. s.</i>	5 (5)	4.3±0.3	55±0.6	74±6	79±4	1.51±0.11	1.19±0.16	0.34±0.01	1.53±0.17	21.9±3.5
<i>P. c.</i>	8 (4)	0.96±0.1	36±0.6	41±3	40±2	2.14±0.10	2.33±0.22	0.30±0.01	2.62±0.21	67.4±8.9
<i>A. g.</i>	2 (1)	0.63	34	40	38	2.05	2.12	0.22	2.33	60.6
Peak V _t										
<i>O. s.</i>		24.4	108	91	86	2.88	4.15	0.49	4.64	50.9
<i>H. c.</i>		8.7	70	75	81	1.99	1.98	0.59	2.57	34.2
<i>H. s.</i>		4.7	58	77	69	1.93	1.86	0.40	2.26	29.2
<i>P. c.</i>		0.85	38	36	36	2.42	2.92	0.33	3.24	90.6
<i>A. g.</i>		0.63	34	35	34	2.26	2.55	0.29	2.84	80.5

For each species the mean values (±S.E.M.) for all jumps are given followed by the values for the jumps with peak takeoff velocities.

*Species tested: *O. s.*, *Osteopilus septentrionalis* (Duméril and Bibron); *H. c.*, *Hyla cinerea* (Schneider); *H. s.*, *Hyla squirella* Bosc; *P. c.*, *Pseudacris crucifer* (Wied-Neuwied); *A. g.*, *Acris gryllus* (LeConte).

†Number of jumps (number of animals).

‡Predicted contact time from equation 6.

t_c, contact time; L_{hl}, hindlimb length; V_t, takeoff velocity estimated as the average value for five frames centered on the frame at which takeoff occurred; W_k, kinetic energy of the center of mass at takeoff; W_p, potential energy of the center of mass at takeoff; W_j, total energy of the center of mass at takeoff; Ẇ_j, average power expended during takeoff.

Table 2. *Jumping performance at 20 °C in hylid frogs estimated from the mean maximum jumping distances and morphological variables reported by John-Alder et al. (1988)*

Species*	M_b (g)	L_{sv} (m)	L_{hl}^\dagger (m)	L_j (m)	Calculated values				
					$L_{j,l}$ (m)	V_t (m s ⁻¹)	t_c (s)	W_j (J kg ⁻¹)	\dot{W}_j (W kg ⁻¹)
<i>O. s.</i>	17.66	0.063	0.100	0.949	0.787	2.81	0.082	4.66	56.7
<i>H. c.</i>	4.02	0.042	0.061	0.528	0.428	2.07	0.068	2.59	37.9
<i>H. s.</i>	2.31	0.031	0.046	0.460	0.384	1.96	0.054	2.25	41.5
<i>P. c.</i>	1.40	0.027	0.041	0.560	0.494	2.22	0.042	2.75	64.7
<i>A. g.</i>	0.47	0.022	0.040	0.702	0.636	2.52	0.037	3.44	93.8

For each species, the longest jump by each of 5–10 animals was recorded for a series of jumps and these maximal values were averaged. These jumps were recorded from a different series of animals from those filmed in the present study and thus the masses reported differ from those in Table 1.

*See Table 1 for key to abbreviations of species names.

†Hindlimb length was estimated from the ratios of hindlimb length to snout–vent length determined on the sample of animals used in this study.

M_b , body mass; L_{sv} , snout–vent length; L_{hl} , hindlimb length; L_j , total jumping distance; $L_{j,l}$, level jumping distance calculated from equation 4; V_t , takeoff velocity calculated from equation 5; t_c , contact time calculated from equation 6; W_j , total work in jumping estimated from equation 3; \dot{W}_j , average power during takeoff calculated from equation 7.

One jump recorded on an *Osteopilus* provided a particularly clear record and was analyzed further to examine the distribution of power output during the jump. This jump was parallel to the focal plane of the camera with a takeoff angle of 30°. The takeoff velocity in this jump was about 2.5 m s⁻¹ (somewhat less than the maximum takeoff velocity of 2.9 m s⁻¹ recorded in another jump by the same animal). The accuracy of our calculations of force and power depends on the accuracy of our polynomial smoothing of the position data (Fig. 1). The adequacy of these curves can be at least partially assessed by comparing them with velocities calculated directly from the position data with only minimal smoothing (Fig. 2A). The two determinations of velocity agree quite closely. Horizontal and vertical velocities rose slowly for the first 50 ms of the jump and then increased rapidly until takeoff at about 120 ms (Fig. 2A). Forces calculated from these data display a similar time course to those recorded by Calow and Alexander (1973). Early in the jump, the forces exerted on the ground are low and they then increase to a peak before falling rapidly as the frog approaches takeoff (Fig. 2B). The total power required for the jump is calculated as the sum of the powers required to accelerate the frog upwards and forwards (Fig. 2C). The maximum body-mass-specific power output during this jump was about 73 W kg⁻¹. The average power during the entire jump was 32 W kg⁻¹, or 44% of the peak value. These calculations should be taken as an approximate confirmation of the pattern of force application documented by Calow and Alexander (1973). However, the estimates of force from the films are subject to substantial errors early in the jump when the velocities are low. The exact shape of the force and power curves also depends critically on the fitting procedure used to produce

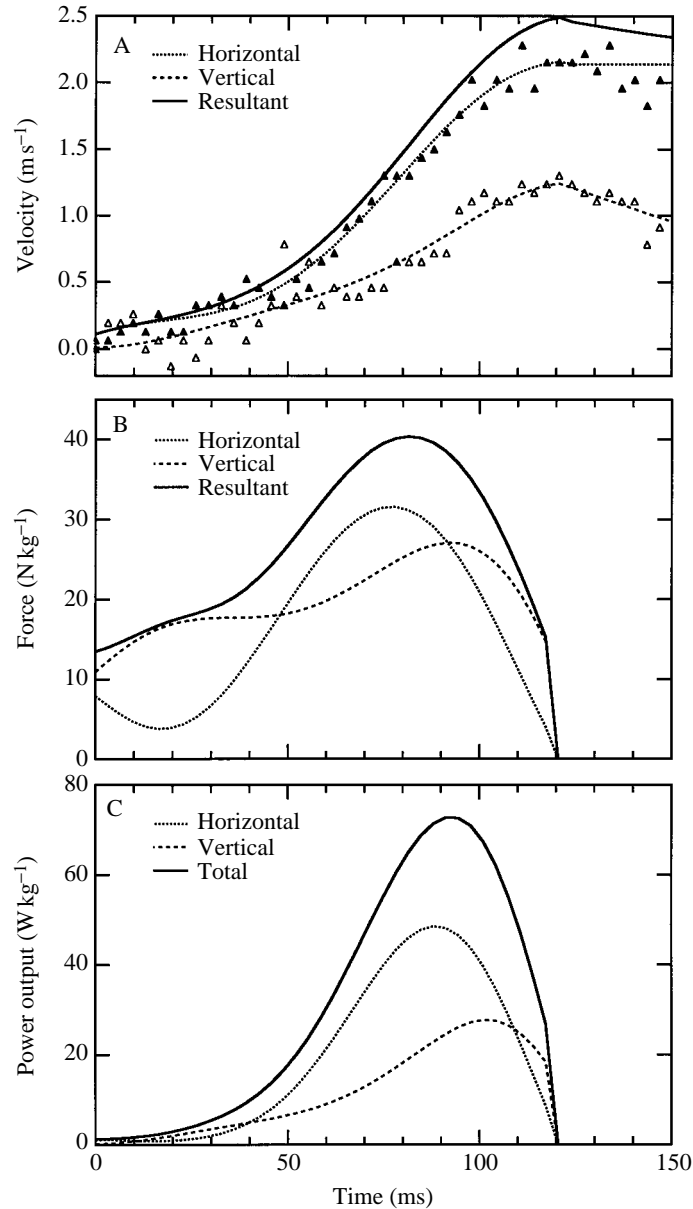


Fig. 2. Velocity (A), force (B) and power output (C) during a jump by an *Osteopilus septentrionalis*. The individual points for horizontal and vertical velocity represent velocities calculated from a three-point running average of the change in position recorded directly from the films. The smooth curves for horizontal and vertical velocities up to the point of takeoff were calculated from eighth-order polynomial curves fitted to the position data (Fig. 1). After takeoff, the smooth horizontal velocity was continued by assuming a constant value and the smooth vertical velocity was continued with the assumption that velocity declined due to the downward acceleration of gravity. Horizontal and vertical forces were calculated by differentiating the smooth velocity curves. Horizontal and vertical power are the product of the appropriate velocity and force. The resultant values for velocity and force were determined by the pythagorean theorem. Total power is the sum of the horizontal and vertical powers.

the smoothed velocity curves. However, these curves appear to describe the data well, and any errors are unlikely to influence the major conclusions drawn here.

Discussion

Calculation of power output from jumping distance depends on accurately estimating contact time. Our filming data (Table 1) reveal that contact time varies with takeoff velocity, as predicted by equation 6. Larger discrepancies were found for jumps with low takeoff velocities. For these jumps, the predicted contact time was always longer than the actual time, reflecting the incomplete extension of the hindlimbs. Our results confirm the power outputs estimated on the basis of jumping distance (Tables 1 and 2). This confirmation is due to the fact that the contact times estimated from equations 4–6 are quite close to those measured from the films. The mean power, considering all of the jumps filmed, was lower than that estimated from the mean maximal jumping distances reported by John-Alder *et al.* (1988). However, frogs undertake only a few maximal jumps in any experimental series (e.g. Zug, 1978), and thus John-Alder *et al.* (1988) followed the standard practice of reporting the maximal distance jumped by each frog in a series of jumps. Using the values from the best jumps we filmed results in much more comparable values. Only one species (*Hyla squirella*) performed much worse during our filming study and one (*Pseudacris crucifer*) performed much better.

These data on jumping performance of hylids confirm that average power output during jumping by anurans is impressively high (Marsh, 1993). Relating these data to muscle power output requires data on the mass of muscle that powers the jump. We did not determine muscle mass on the specific animals used in our study because they were also being used for other measurements. Three estimates are available for total hindlimb mass as a percentage of body mass in hylid frogs: *Pseudacris crucifer* 14%, *Hyla versicolor* 17% and *Osteopilus septentrionalis* 16% (Taigen *et al.* 1985; Marsh and Taigen, 1987; R. L. Marsh, unpublished data). Probably at most 80–85% of this total muscle mass represents muscles that participate in the jump (Matsui, 1978; Marsh, 1993), but the individual muscles have not been weighed in hylids. Even if the high value of 17% is taken as the mass of muscle powering jumping in hylids, the muscle-mass-specific average power output during jumping in these small tree frogs is estimated to be between 225 and 550 W kg⁻¹ at 20 °C.

The highest power outputs recorded during *in vitro* isotonic contractions of anuran hindlimb muscles at 20 °C are approximately 350 W kg⁻¹ (Cecchi *et al.* 1978; Lännergren *et al.* 1982). Most estimates are lower, with a mean of approximately 270 W kg⁻¹ (Marsh, 1993). Isotonic power output in muscles from hylids weighing 5–30 g is unexceptional (*Hyla versicolor* sartorius, 205 W kg⁻¹; *Osteopilus septentrionalis* sartorius, 225 W kg⁻¹; R. L. Marsh, unpublished results). Maximal isotonic shortening velocity (V_{\max}) increases with decreasing body mass (Marsh, 1994), but the exponent is low ($V_{\max} \propto \text{body mass}^{-0.1}$). Thus, muscles from even the smallest species used in this study are unlikely to produce much greater isotonic powers than those already recorded. The production of an average power even equal to the maximal isotonic power seems remarkable, given that jumping results from the action of a complex set of muscles acting

in concert and that these muscles will require some time after activation to reach maximum power output.

Power output during jumping is even more remarkable when it is considered that the values calculated above are for average power expended during the takeoff phase. Peak power during takeoff is expected to be approximately twice the average power (Bennet-Clark, 1977). Our analysis of a single jump by an *Osteopilus* suggests that average power is 44 % of the peak value, and data of Hirano and Rome (1973) yield a similar estimate of 47 %. Thus, peak muscle-mass-specific power output during jumping by some hylid frogs can be as high as 1000 W kg^{-1} , exceeding by a considerable margin the power available from direct muscle contraction.

What factors might explain power output in excess of the maximum isotonic power? A likely mechanism is the use of elastic energy storage during jumping (Bennet-Clark, 1977). The amount of work produced by the hindlimb muscles ($13\text{--}27 \text{ J kg}^{-1}$ if the jumping muscles make up 17 % of the body mass) is consistent with the performance of isolated frog muscles (e.g. Gibbs and Chapman, 1974). Elastic storage allows this work to be performed over a period of time compatible with the shortening velocity of the muscles. The high peak power late in takeoff could be explained by the redistribution of power output by elastic elements. The muscle fibers may shorten steadily throughout the contact phase, but the application of this power externally may be modified by elastic elements, for example tendons, in series with the muscles. Elastic elements stretched early in the jump could shorten late in the contact phase, providing the peak power required. Of course, the redistribution of energy during the contact phase cannot explain the fact that in some cases average power also exceeds the power expected from the muscles based on isotonic contractions. Explaining the high average power on the basis of elastic energy storage would require the energy storage to occur before movement begins, as is the case in some insects (Bennet-Clark, 1977). Intriguingly, the masses and jumping distances of the smaller hylids studied are similar to those of the locusts studied by Bennet-Clark (1975). The insects studied to date all show some sort of anatomical 'catch' that helps prevent movement during the period when the elastic elements are prestretched. There is no current evidence to suggest that there is a discrete anatomical 'catch' in anurans that could prevent hindlimb movement during contraction of the leg extensors prior to the jump. However, a physiological 'catch' could occur if the unfavorable mechanical advantage of the extensors early in the jump and/or the co-contraction of antagonists delayed the beginning of takeoff. A similar mechanism exists in locusts (Bennet-Clark, 1975). Alternatively, the muscles may deliver more power when shortening under *in vivo* conditions, which almost certainly are not isotonic. Currently available data do not allow the assessment of these alternatives in hylid frogs. Further analysis of possible sites for elastic storage and records of jumping, including electromyograms of antagonistic muscles and measurements of muscle length changes, should help to clarify these alternatives.

We thank Peter J. Morin for loaning us the animals used in this study. The research was supported by a grant awarded to R.L.M. from the National Institute of Arthritis and Musculoskeletal Diseases (AR-39318), and a grant awarded to H.B.J. from the Charles

and Johanna Busch Memorial Fund administered through Rutgers University. The comments of two anonymous reviewers significantly improved the manuscript.

References

- ALTEVOGT, R., HOLTSMANN, H. AND KASCHEK, N. (1986). High frequency cinematography studies on locomotion and preying in Indian skitter frogs *Rana cyanophlyctis* Schneider. *J. Bombay nat. Hist Soc.* **83** (Suppl.), 102–111.
- BENNET-CLARK, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. exp. Biol.* **63**, 53–83.
- BENNET-CLARK, H. C. (1977). Scale effects in jumping animals. In *Scale Effects in Animal Locomotion* (ed. T. Pedley), pp. 185–201. New York: Academic Press.
- CALOW, L. J. AND ALEXANDER, R. MCN. (1973). A mechanical analysis of the hind leg of a frog (*Rana temporaria*). *J. Zool. Lond.* **171**, 293–321.
- CECCHI, G., COLUMO, F. AND LOMBARDI, V. (1978). Force–velocity relation in normal and nitrate-treated frog single muscle fibers during the rise of tension in isometric tetanus. *J. Physiol., Lond.* **285**, 257–273.
- EMERSON, S. B. (1978). Allometry and jumping in frogs: helping the twain to meet. *Evolution* **32**, 551–564.
- GANS, C. (1961). A bullfrog and its prey: a look at the biomechanics of jumping. *Nat. Hist.* **70**, 26–37.
- GIBBS, C. L. AND CHAPMAN, J. B. (1974). Effects of stimulus conditions, temperature, and length on the energy output of frog and toad sartorius. *Am. J. Physiol.* **227**, 964–971.
- GRAY, J. (1968). *Animal Locomotion*. London: Weidenfeld and Nicolson.
- HIRANO, M. AND ROME, L. C. (1984). Jumping performance of frogs (*Rana pipiens*) as a function of muscle temperature. *J. exp. Biol.* **108**, 429–439.
- HIRSCH, W. (1931). Zur physiologischen Mechanik der Froschsprünge. *Z. vergl. Physiol.* **15**, 1–49.
- JOHN-ALDER, H. B., MORIN, P. J. AND LAWLER, S. (1988). Thermal physiology, phenology and distribution of tree frogs. *Am. Nat.* **132**, 506–520.
- LÄNNERGRÉN, J., LINDBLÖM, P. AND JOHANSSON, B. (1982). Contractile properties of two varieties of twitch fibers in *Xenopus laevis*. *Acta physiol. scand.* **114**, 523–535.
- MARSH, R. L. (1994). Jumping ability of anuran amphibians. In *Advances in Veterinary Science and Comparative Medicine: Comparative Vertebrate Exercise Physiology* (ed. J. H. Jones). New York: Academic Press (in press).
- MARSH, R. L. AND TAIGEN, T. L. (1987). Properties enhancing aerobic capacity of calling muscles in gray tree frogs *Hyla versicolor*. *Am. J. Physiol.* **252**, R786–R793.
- MATSUI, M. (1978). Correlation between relative weights of hindlimb muscles and locomotor patterns in Japanese anurans. *Contr. Biol. Lab. Kyoto Univ.* **25**, 223–240.
- TAIGEN, T. L., WELLS, K. D. AND MARSH, R. L. (1985). The enzymatic basis of high metabolic rates in calling frogs. *Physiol. Zool.* **58**, 719–726.
- WLEDGE, R. C., CURTIN, N. A. AND HOMESHER, E. (1985). *Energetic Aspects of Muscle Contraction*. New York: Academic Press.
- ZUG, G. R. (1978). Anuran locomotion – structure and function. II. Jumping performance of semiaquatic, terrestrial and arboreal frogs. *Smithson. Contrib. Zool.* **276**, 1–31.