

JUMPING PERFORMANCE OF FROGS (*RANA PIPIENS*) AS A FUNCTION OF MUSCLE TEMPERATURE

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Accepted 7 September 1983

SUMMARY

This study was performed to determine whether or not the power generated by frog muscles during maximal jumps increases two- to three-fold with a 10°C increase in temperature as it does in isolated preparations. We found that peak power increased 2.7-fold between 14 and 25°C, and then remained constant to 30°C. During jumps at 14 and 25°C, the extensor muscles of the legs appeared to generate the same power as the maximum power output found in isolated frog muscle preparations, thus suggesting that the total cross section of the extensors is active during maximal jumps. We also found that jump distance was linearly related to peak power generation.

INTRODUCTION

An apparent inconsistency exists between the mechanics of frog muscle studied in isolated preparations and their performance *in vivo*. The maximum mechanical power developed by frog muscle preparations increases by a factor between 1.8 and 3 for each 10°C increase in muscle temperature over the range of temperatures between 0 and 25°C (Hill, 1938; Rome, 1983). It seems reasonable to extrapolate these results to the whole animal and to expect that the maximum distance a frog could jump would increase with muscle temperature in some similar fashion. Huey (1975) reported that jumping distance is nearly independent of temperature between 10 and 25°C. It is hard to reconcile this observation with the isolated muscle experiments.

In this study we set out to explain this paradox by determining how the mechanical power developed by frog muscles during 'maximal' jumps changed with temperature. We felt that these measurements should explain whether mechanical performance of *in vitro* and *in vivo* frog muscle preparations differ, and, if so, how.

MATERIALS AND METHODS

Animals

Eight male *Rana pipiens* were obtained from the Lake Champlain frog farm (Alburg, Vt.). The frogs were kept in a large tub. Half of the tub contained a pool of water

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Key words: Biomechanics, muscle recruitment, muscle power.

that was continually refreshed, the other half was dry. Live crickets were fed to the frogs twice weekly. Room and water temperature were maintained at 18–22 °C.

Procedures

Frogs were stimulated to jump 'maximally' in a series of experiments while muscle temperature was varied from 14 to 30 °C. The forces exerted on the ground during these jumps were measured using a force platform. The velocity of take-off, hop distance and mechanical power were calculated from the instantaneous measurements of force during the jump.

Muscle temperature of the frogs was varied by equilibrating the frogs to different ambient temperatures. Frogs were kept at each experimental temperature for 18 h prior to jumping. The cloacal temperature of each frog was measured before and after jumping using a small vinyl-coated thermocouple (Westcor Model TH60, accuracy ± 0.2 °C). The average difference between the pre- and post-jump temperatures was 0.6 °C and the maximum difference was 3 °C.

Each frog jumped 10–15 times at each temperature and only the best jump was used. In order to obtain 'maximal' jumps, frogs were placed on an electrified copper grid that was attached to the force plate. Stimulus voltage (Grass Stimulator Model S44) to the grid was increased until jump distance became independent of voltage. It was found that a stimulus of about 30 V elicited a 'maximal' jump.

The force platform (Fig. 1) measured the forces exerted in the horizontal (x) and vertical (y) planes. The force plate had two strain gauge instrumented spring blades at 90° orientation to each other at each corner of the force platform (Heglund, 1981). Forces in the lateral (z) axis, were assumed to be insignificant because the frogs were made to jump in a narrow runway (10 cm in width). Therefore, in a typical jump of 30 cm, if the frog were to stray the maximum 5 cm laterally from the forward path direction, the difference in distance jumped (as well as in peak force) would be less than 1.5 %.

The signals from the force plate strain gauges were amplified by a Vishay Strain Gauge Conditioner (Model 2120) and high frequency noise was filtered with a low pass filter. The vertical and horizontal force record signals were observed on two channels of an oscilloscope and recorded on an FM tape recorder (Lockheed Model 417). The stimulator current across a 100 Ω resistor was also recorded on a third channel of the tape recorder.

The force plate was calibrated for each set of jumps. The peak force never exceeded 1.5 N in either the horizontal or vertical component of the jump. The natural frequency of the plate was 170 Hz in the vertical plane and 240 Hz in the horizontal plane. There was less than 3 % cross-talk between the two components. The accuracy of the measurements was better than ± 5 %.

The force records were played into a Digital PDP-11 computer (using an analogue-to-digital converter) which sampled the instantaneous force in the vertical (F_v) and horizontal (F_h) planes at 5-ms intervals.

The instantaneous acceleration in the vertical (a_v) and horizontal (a_h) planes was calculated by the computer using equations 1 and 2.

$$a_v = \frac{F_v - mg}{m} \quad (1)$$

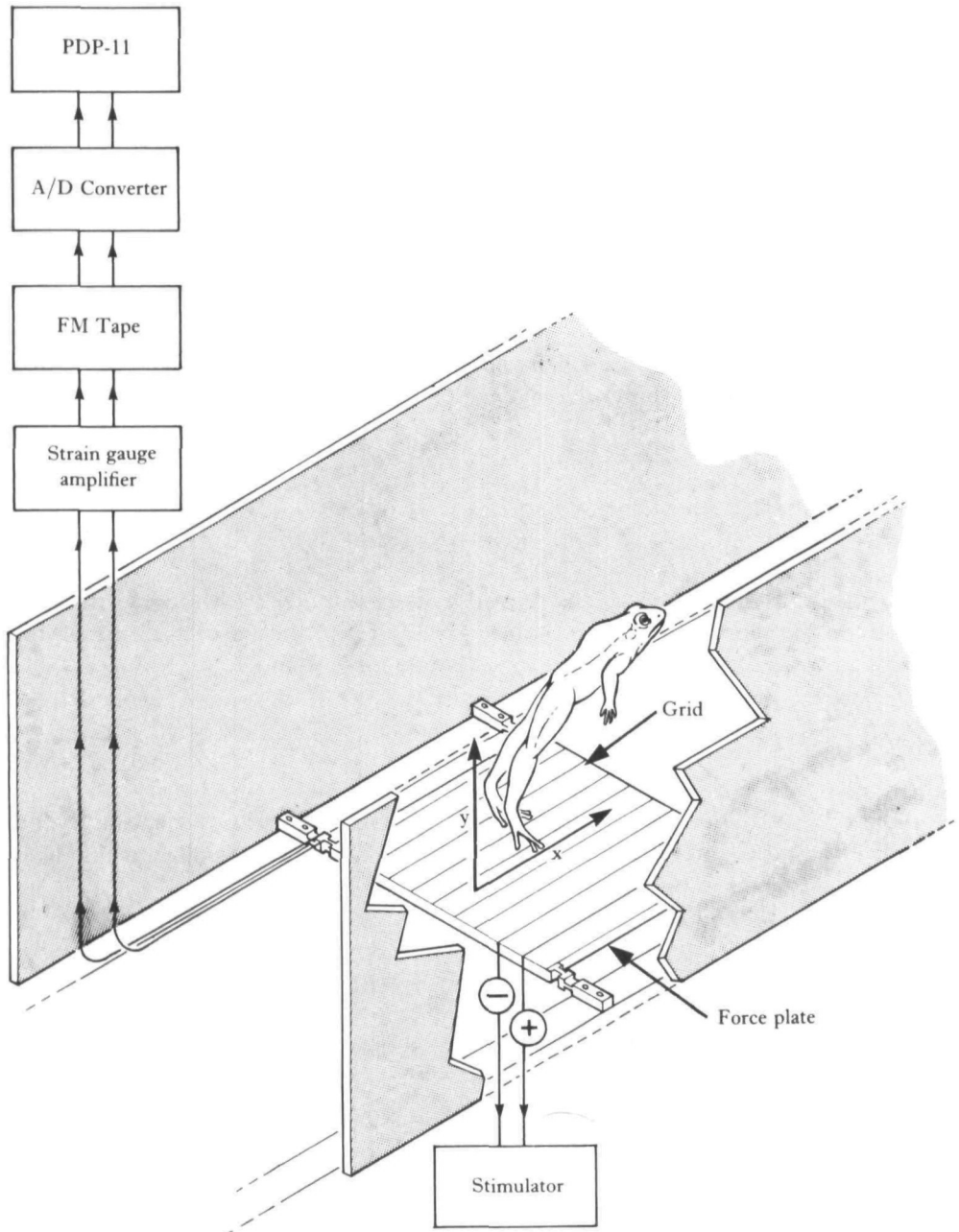


Fig. 1. Apparatus for measuring the mechanics of frog jumping. The frogs were made to jump down the runway by delivering the stimulus to the grid on which they were standing. The forces exerted on the ground during the jump were measured by the force platform and were saved for further analysis with the FM tape recorder. The force records were subsequently played into the A/D converter and were integrated by the PDP-11 computer to give the velocity, distance and power generation of the jump.

$$a_h = \frac{F_h}{m}, \quad (2)$$

where m is the mass of the frog and g is the gravitational constant.

The instantaneous velocities in the vertical (V_v) and horizontal (V_h) planes were calculated by the computer using equations 3 and 4.

$$V_v = \int_0^t a_v dt \quad (3)$$

$$V_h = \int_0^t a_h dt. \quad (4)$$

The instantaneous displacement in the vertical (y) and horizontal (x) directions was calculated by the computer using equations 5 and 6.

$$y = \int_0^t V_v dt \quad (5)$$

$$x = \int_0^t V_h dt. \quad (6)$$

The jump distance x_j was calculated by the computer as the sum of the displacement of the centre of mass at the time of take-off (x_T) and the displacement while the animal was in the air (x_A) according to equations 7, 8 and 9.

$$x_j = x_T + x_A \quad (7)$$

$$x_A = V_{hT} \cdot t_A, \quad (8)$$

where V_{hT} is the velocity of the centre of mass in the horizontal plane at the time of take-off, and t_A is the time the animal is in the air and is calculated as the quadratic root of equation 9.

$$\left[-\frac{1}{2}(9.8)t^2 + V_{vT} \cdot t + y_T \right] = 0, \quad (9)$$

where V_{vT} is the vertical velocity at take-off and y_T is the vertical displacement of the centre of mass at take-off. Instantaneous power (P) developed during the jump was calculated using equation 10.

$$P = m g V_v + \frac{0.5 m [V^2(t) - V^2(t - 0.005 s)]}{0.005 s}, \quad (10)$$

where V is the vector sum at any instant of V_v and V_h and 0.005 s was the sampling interval. Peak power was estimated by averaging the power generated during the three 5-ms time periods in which it was largest. This averaging was done to reduce noise-related errors.

RESULTS

Frogs generated greater forces but over shorter periods of time as muscle temperature increased. Average peak force increased by about 70 % between 14 and 25 °C

and then dropped, though not significantly, at 30 °C (Fig. 2A). The average time the forces were exerted during the jumping fell from 0.22 s to 0.12 s as the temperature increased from 14 to 30 °C (Fig. 2B).

Jump distance increased by 14 cm (about 60 %) as the frog's temperature increased from 14 to 25 °C, primarily because of an increase in the duration of the aerial phase of the jump (t_A). Table 1, however, shows that there was a great deal of variation between frogs. Jump distance equals the sum of the distance travelled prior to take-off (x_T) and the distance travelled after take-off (x_A ; equation 7). Changes in x_T cannot account for the large difference in jump distance because it varies only by

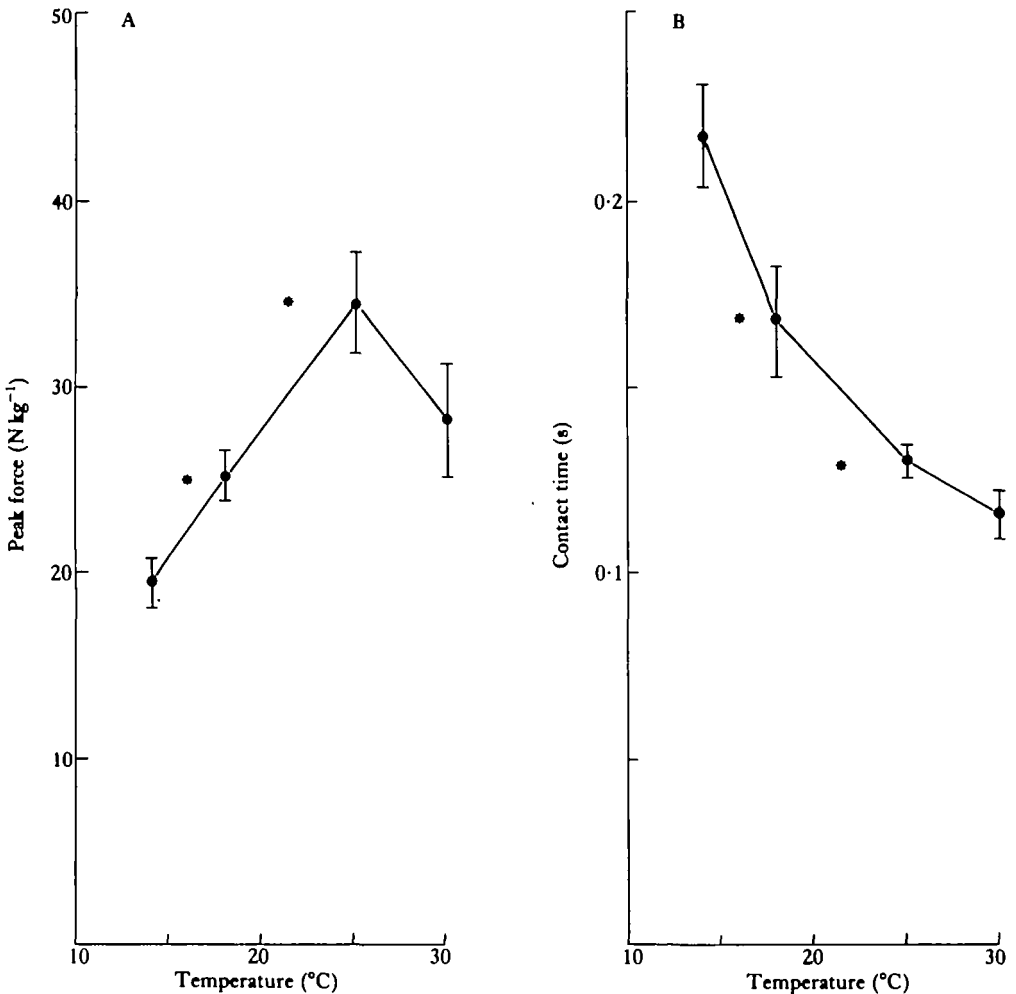


Fig. 2. As muscle temperature of frogs increased, they generated greater forces over shorter time periods. (A) Peak force (per kg body weight) generated during maximal jumps are reported as a function of temperature. At each temperature, the mean value of peak force from eight animals is shown with standard error bars. The asterisks signify statistical differences (at 95 % confidence level) between mean values at different temperatures. (B) The time over which forces were exerted on the ground decreased with increasing temperature. The data in B are presented in the same format as in A.

Table 1. *Maximum jump distance as a function of temperature*

Frog No.	Jump distance (m)			
	14°C	18°C	25°C	30°C
1	0.19	0.37	0.25	0.19
2	0.28	0.25	0.44	0.34
3	0.29	0.46	0.47	0.32
4	0.20	0.31	0.29	0.34
5	0.23	0.26	0.36	0.49
6	0.23	0.20	0.31	0.45
7	0.33	0.18	0.47	0.20
8	0.19	0.17	0.46	0.17
	0.24(±0.02)	0.27(±0.04)	0.38(±0.03)	0.31(±0.04)

Jump distance was calculated by computer (see Material and Methods) from force records. The longest jump from 10–15 attempts is shown for each frog at four experimental temperatures. Means are reported with s.e. in parentheses.

2.5 cm between 14 and 25°C (Fig. 3A). The increase in jumping distance was thus due entirely to a two-fold increase in distance travelled while in the aerial phase (x_A ; Fig. 3A). The horizontal take-off velocity (V_{hT}) increased by only 23% over this temperature range (Fig. 4A), and thus explains only a small portion of the increase in x_A (see equation 8). Fig. 4B shows that t_A increased almost two-fold between 14 and 25°C and was mainly responsible for the increase in x_A .

The increase in t_A was due primarily to an increase in vertical take-off velocity (V_{vT}) between 14 and 25°C (Fig. 4D). Although y_T (take-off height) increased significantly (3 cm) between 14 and 25°C (Fig. 4C), this would account for only a 20% increase in t_A (equation 9).

The three-fold increase in V_{vT} is due to an almost five-fold increase in average vertical acceleration (\bar{a}_v). V_{vT} is equal to $\int_0^t a_v dt$, or more simply, \bar{a}_v times contact time. As noted, contact time decreased by 50% and thus the \bar{a}_v must increase approximately five-fold. V_{hT} shows relatively little temperature dependence because the increase in a_h just matches the decrease in contact time.

The increase in both the force generated by the muscle and the velocity at which the muscles are shortening requires that muscle power output should increase. Fig. 3B shows that peak power output during the jump increased about 2.7-fold between 14 and 25°C, and then fell, though not significantly, at 30°C.

DISCUSSION

Muscle function: in vivo versus in vitro

The performance of *Rana pipiens* muscles during jumping closely parallels their performance *in vitro*. To a first approximation, the total cross section of the extensor muscles is active and generates maximum power. This observation follows from the comparison of maximum power generation *in vivo* and *in vitro*. Rome (1983) found that the maximum power generated by the sartorius muscle was 138 W kg⁻¹ at 15°C and 250 W kg⁻¹ at 25°C. In these experiments we found that peak power per kg body weight generated during the jump was 14.4 W at 14°C and 39 W at 25°C. Dissection

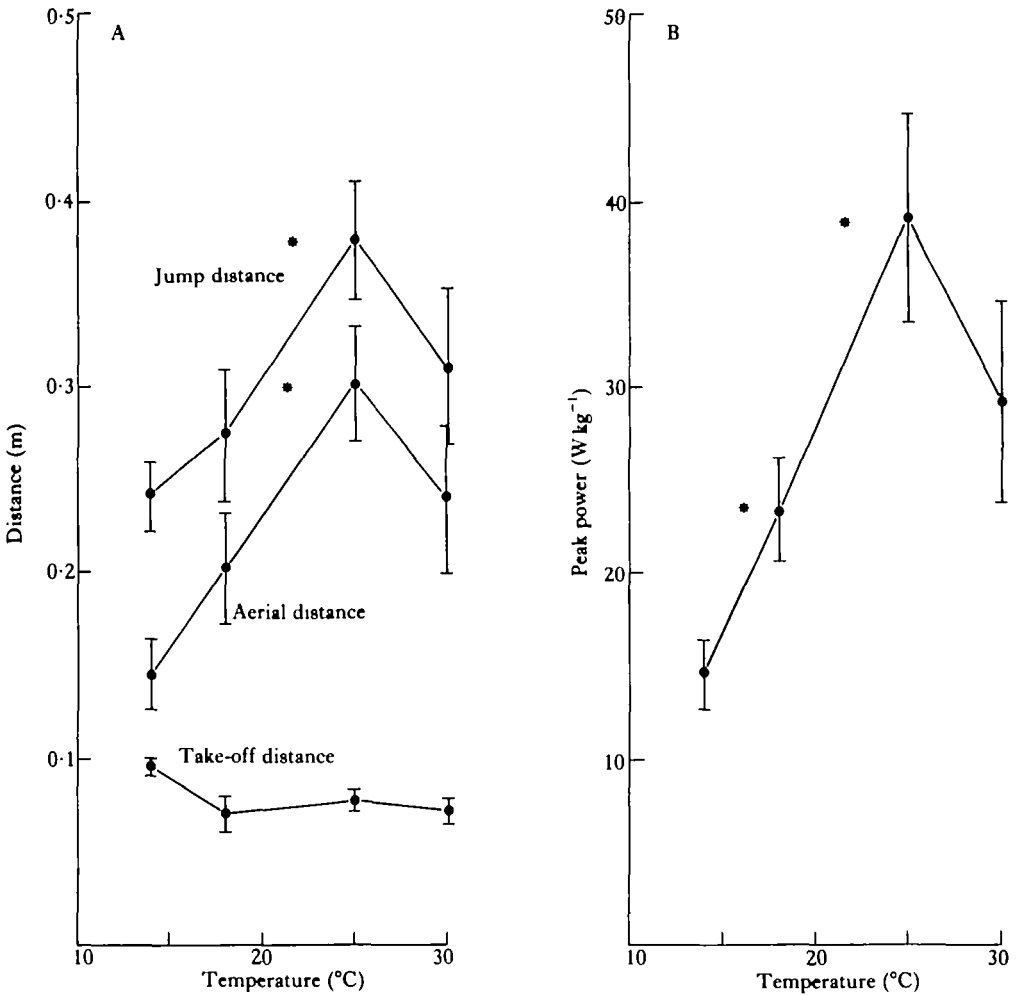


Fig. 3. Both the distance frogs jumped and the power generated by their muscles increased between 14 and 25 °C. (A) Jump distance (x_j) is equal to the sum of the distance travelled during the aerial phase (x_A) and the distance travelled prior to take-off (x_T). The increase in x_j between 14 and 25 °C is due to an increase in x_A , as x_T remained constant over the temperature range. (B) Peak power (per kg body weight) is shown as a function of temperature. The data in both figures are presented in the same format as in Fig. 2.

of the muscles that are thought to provide most of the power during jumping (Calow & Alexander, 1973) namely the cruralis, semitendinosus, plantaris longus, gluteus magnus, semimembranosus and gracilis major, reveal that they make up approximately 14% of the animal's total body weight. Thus the power generation of these muscles was about $100\ W\ kg^{-1}$ at 14 °C and $272\ W\ kg^{-1}$ at 25 °C. The similarity of the power output per kg of muscle of the 'maximally' stimulated *in vitro* muscle preparation to that observed in the extensor muscles of the jumping frogs suggests that *all* of the muscle fibres were active and generating maximum power during the jump. It further suggests that the muscles are arranged in a manner that enables all fibres to contribute simultaneously to power output.

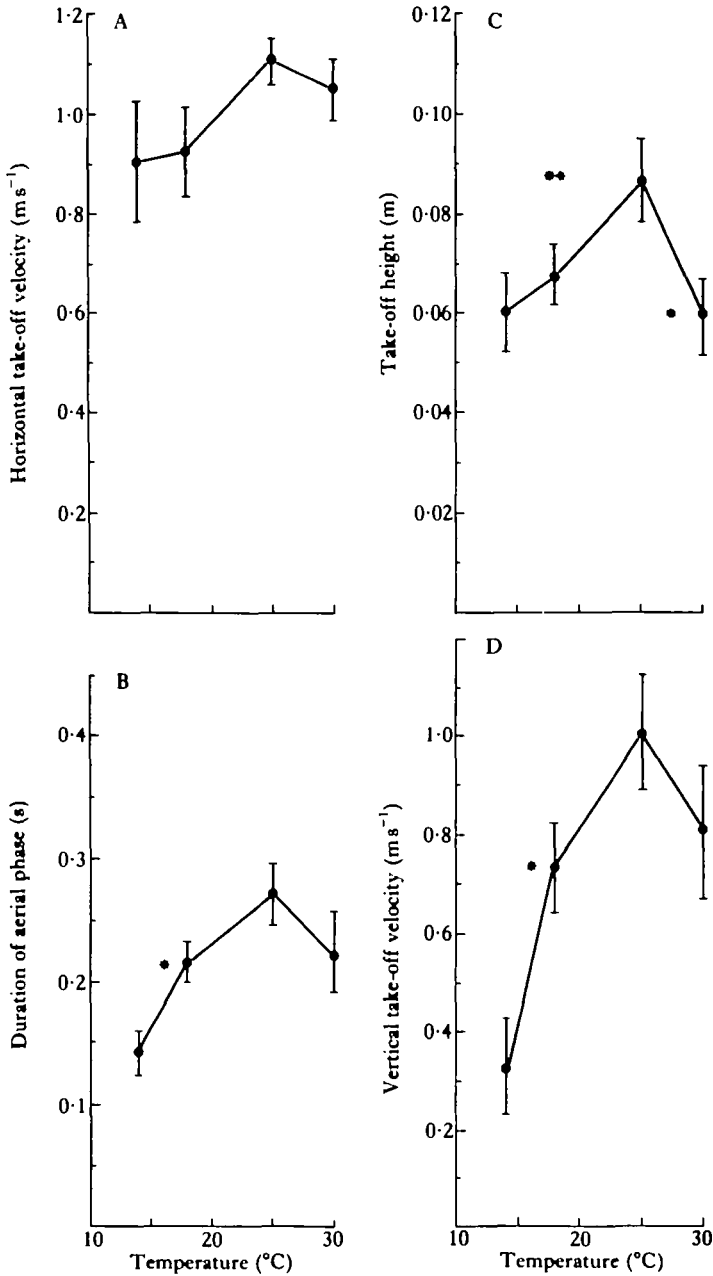


Fig. 4. The increase in distance travelled during the aerial phase (x_A) was due to a longer duration of the aerial phase (t_A). (A) x_A = the horizontal take-off velocity (V_{HT}) \times t_A . V_{HT} increases only slightly between 14 and 25 °C whereas t_A increases about two-fold (B). Although take-off height (C) increases significantly between 14 and 25 °C (double asterisks), the increase in t_A is primarily due to the large increase in vertical take-off velocity (D). All data are presented in the same format used in Fig. 2.

The absence of a continued increase in muscle power as *Rana pipiens* temperature increased from 25 to 30 °C is probably due to a decrease in fine motor control. When body temperature is increased to 34 °C, the frogs lose the ability to right themselves, and this temperature has been called their 'critical thermal maximum' (Brattstrom & Lawrence, 1962). It is likely that there would be a gradual loss of motor control as the critical thermal maximum is approached.

Relationship between jump distance and power output

Jump distance appeared to be nearly linearly related to peak power generated during the jump (Fig. 5). The large y-intercept for jump distance results in the difference in Q_{10} between peak power ($Q_{10} = 2.7$) and jump distance ($Q_{10} = 1.6$). In a plot of the distance travelled in the aerial phase (x_A), as a function of muscle power, the intercept was much reduced, showing that a large part of the intercept observed in the jump distance *versus* muscle power relationship is due to the distance travelled prior to take-off (x_T). x_T consists of simply falling forward which requires very little power.

The increase in x_A with peak power appears to be due to a concomitant increase in vertical take-off velocity (V_{VT}). The mechanical power necessary to maintain a constant vertical velocity against the gravitational field is directly proportional to velocity. Therefore, animals that can generate power at higher levels, can maintain larger vertical velocities, and thus achieve longer aerial phases (t_A) and longer jumps. This relationship does not hold however, if the animals jump at too steep an angle. Fig. 5 shows that jumps in which the take-off angle exceeds 50° (indicated as open symbols) fall considerably below the regression line determined for jumps of less than 50°. This is because in a steep jump a high rate of power generation will lead to a large vertical velocity and a long duration of the aerial phase, but does not lead to a long jump because the horizontal take-off velocity is low.

Jumping performance as a function of temperature

The results of this experiment are in disagreement with those of Huey (1975). Although we both found that jump distance increased with temperature to a certain point and thereafter decreased, Huey found that jump distance varied less than 15% between 10 and 25 °C, whereas we found that between 14 and 25 °C, there was a 60% increase in jump distance.

The differences in the results might represent a species difference. Huey used *Rana clamitans* and we used *Rana pipiens*. The close agreement of our force plate data with those collected at 22 °C on *Rana temporaria* (Calow & Alexander, 1973) suggests that there is little difference between ranid species. Calow & Alexander found that (21–28 g) *Rana temporaria* generated a peak force of 29 N per kg body weight and jumped about 0.4 m.

The data collected in this study suggest that warm frogs might be substantially better than cold frogs at escaping from predators. Not only do warm frogs jump further, they also spend less time on the ground before take-off. It is also unlikely that long-term exposure to cold temperatures would reduce the advantage of warm frogs. Rome (1983) found that there was no difference in the mechanical power output of muscles from frogs acclimated to 12 and 28 °C for 8 months, nor were differences in

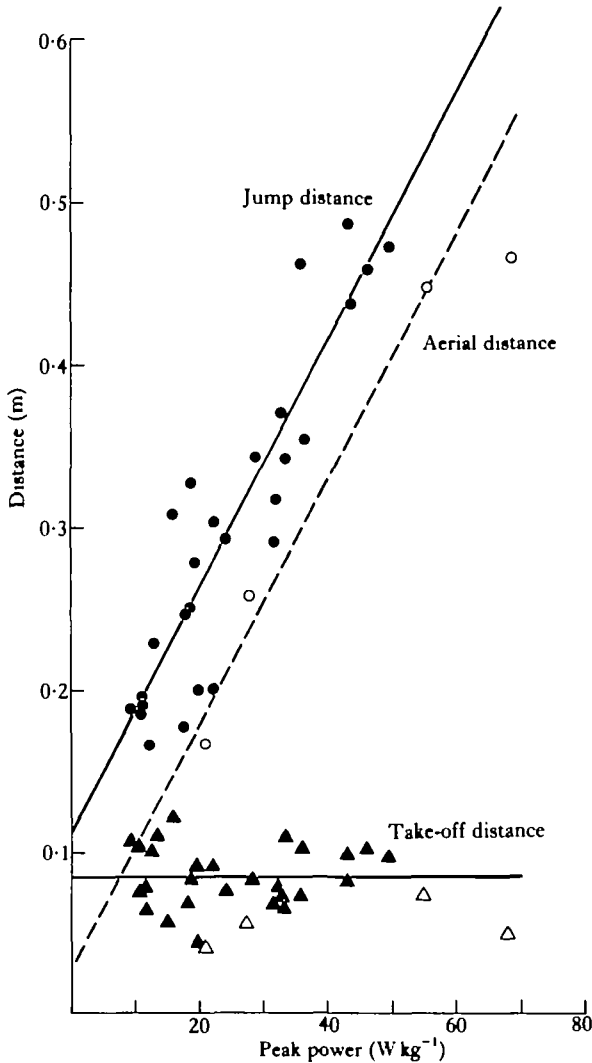


Fig. 5. Jump distance was linearly related to peak power generation during jumps. The data for jump distance (x_j -circles) and distance travelled prior to take-off (x_T -triangles) are shown as a function of peak power generated during the jump. Regression lines (solid) are shown for both relationships. The data for distance travelled during the aerial phase (x_A) are omitted for clarity, but the regression line (dashed) is shown. Data from jumps where the take-off angle exceeded 50° are shown as open symbols and are not included in the regression equations. The equations were as follows: $x_j = 0.0076 \times \text{power} + 0.112$, $r^2 = 0.84$; $x_A = 0.0076 \times \text{power} + 0.029$, $r^2 = 0.93$; $x_T = 0.000 \times \text{power} + 0.083$.

neuromuscular parameters observed by Grainger & Goldspink (1964) after acclimation. Carp, on the other hand, appear to be able to modify the properties of their muscles during acclimation (Johnston, Davison & Goldspink, 1975) and a corresponding improvement in swimming performance at low temperatures has been observed (L. C. Rome, P. T. Loughna & G. Goldspink, in preparation).

Our results suggest that an animal's maximum locomotory performance may be limited by the temperature dependence of muscle power over certain temperature

ranges. This conclusion is in contrast to the data on submaximal performance of varanid lizards and of carp. Rome (1982), for instance, found that the energetic cost, stride frequency and limb movements of lizards running at 28 and 38 °C was the same. Rome & Loughna (1983) found that tail beat frequency while swimming at a variety of speeds was the same at 10 and 20 °C. The EMG activity of fast and slow fibres in carp suggests that the same mechanical power is achieved at the low temperature as at the warm by a combination of recruiting a greater number of fibres and faster fibre types at the cold temperature. During maximal activity such as in a jump, our results suggest that all the muscle fibres would be active and that the animal cannot rely on differential recruitment patterns to compensate for the temperature effect on muscle power.

The authors thank Professor C. R. Taylor for his guidance and enthusiasm during the experimental work and for his advice during the writing of the manuscript. Laszlo Meszoly drew the figures and Seth Sweet typed the manuscript. The research was supported by NIH Grant No. 5 RO1 AM18140 and NSF Grant No PCM 8119868 to CRT and by an NIH Training Grant No 5 T32 GM 07717.

REFERENCES

- BRATTSTROM, B. H. & LAWRENCE, P. (1962). The rate of thermal acclimation in anuran amphibians. *Physiol. Zool.* **35**, 148–156.
- CALOW, L. J. & ALEXANDER, R. McN. (1973). A mechanical analysis of a hind limb of a frog (*Rana temporaria*). *J. Zool., Lond.* **171**, 293–321.
- GRAINGER, J. N. R. & GOLDSPIK, G. (1964). The effect of adaptation temperature on the properties of nerve-muscle preparations and on the performance of the frog *Rana temporaria*. *Helgol. Wiss. Meeresunters.* **9** No. 1-44202427.
- HEGLUND, N. C. (1981). A simple design for a force-plate to measure ground reaction forces. *J. exp. Biol.* **93**, 333–338.
- HILL, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. B.* **126**, 136–195.
- HUEY, R. B. (1975). Ecology of lizard thermoregulation, Ph.D. thesis, Harvard University.
- JOHNSTON, I. A., DAVISON, W. & GOLDSPIK, G. (1975). Adaptation in Mg²⁺ activated myofibrillar ATPase activity induced by temperature acclimation. *FEBS Letts* **50** (3), 293–295.
- ROME, L. C. (1982). Energetic cost of running with different muscle temperatures in Savannah monitor lizards. *J. exp. Biol.* **99**, 269–277.
- ROME, L. C. (1983). The effects of long-term exposure to different temperatures on the mechanical performance of frog muscle. *Physiol. Zool.* **56**(1), 33–40.
- ROME, L. C. & LOUGHNA, P. T. (1983). The effect of temperature on muscle fiber recruitment of swimming carp. *Fedn Proc. Fedn Am. Socs exp. Biol.* **42**(3), 469.

