

TEMPERATURE, MUSCLE POWER OUTPUT AND LIMITATIONS ON BURST LOCOMOTOR PERFORMANCE OF THE LIZARD *DIPSOSAURUS DORSALIS*

BY STEVEN J. SWOAP¹, TIMOTHY P. JOHNSON², ROBERT K. JOSEPHSON² AND
ALBERT F. BENNETT²

¹*Department of Physiology and Biophysics and* ²*Department of Ecology and
Evolutionary Biology, University of California, Irvine, CA 92717, USA*

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Summary

The mechanical power output of fast-twitch fibres from the iliofibularis of the lizard *Dipsosaurus dorsalis* was measured over a broad body temperature range using the oscillatory work-loop technique. The optimal cycling frequency, that frequency at which mechanical power output is maximal, increases with temperature from 3.3 Hz at 15°C to 20.1 Hz at 42°C. Maximum power output increases with temperature, from 20 W kg⁻¹ at 15°C to 154 W kg⁻¹ at 42°C, the largest power output yet measured using the work-loop technique. At low temperatures (15°C and 22°C), stride frequency during burst running is nearly identical to the optimal cycling frequency for *in vitro* power output, suggesting that maximum power output may limit hindlimb cycle frequency *in vivo*. However, at higher temperatures (35°C and 42°C), the optimal cycling frequency of the isolated muscle is significantly higher than the burst stride frequency, demonstrating that contractile events no longer limit hindlimb cycle frequency. At higher temperatures, it is thus unlikely that the fast-twitch fibres of this muscle *in vivo* attain their potential for maximum power output.

Introduction

Temperature has profound effects on skeletal muscle performance in ectotherms (Bennett, 1984, 1985). Many rate processes of muscle contraction, both isometric and isotonic, are highly temperature-dependent. This thermal dependence is reflected at the molecular level: for example, myosin ATPase activity and Ca²⁺ sequestration by the sarcoplasmic reticulum typically exhibit Q₁₀ values greater than 2 (reviewed in Rall and Woledge, 1990). As body temperatures may vary widely in ectotherms, even over a single diurnal cycle, the thermal dependence of muscle contraction kinetics may be expected to have significant effects on locomotor performance.

The effects of temperature on burst locomotor performance of the desert iguana, *Dipsosaurus dorsalis*, have been documented previously. Hindlimb cycling frequency

during running bursts increases with body temperature to a maximum at 40°C and decreases sharply at higher temperatures (Marsh and Bennett, 1985). 40°C is the animal's preferred body temperature (DeWitt, 1967). Marsh and Bennett (1985) examined the relationship between burst-speed running of the lizard *Dipsosaurus dorsalis* and twitch kinetics of the fast glycolytic (FG) fibres of the iliofibularis muscle (IF). The IF spans both the hip and knee joints and is important in crural flexion and femoral retraction at the onset of the propulsive stroke in the running lizard (Snyder, 1954; Jayne *et al.* 1990). In *Dipsosaurus dorsalis*, the IF consists of approximately 30% slow/tonic fibres recruited during slow locomotor activities and 70% fast fibres (FG) recruited during burst running (Gleeson *et al.* 1980; Jayne *et al.* 1990). At temperatures greater than 25°C, the duration of the power stroke of the hindlimb (half of the full hindlimb cycle duration) is longer than the twitch duration (measured from onset to 50% relaxation) of the FG fibres. Thus, at high temperatures the twitch duration of IF fibres is short enough so that, during running, the muscle may be partially tetanized. However, at temperatures lower than 25°C, the twitch duration is so long that it becomes a potential rate-limiting step in the power stroke/recovery cycle. A similar relationship was also found in locomotor muscles of the western fence lizard, *Sceloporus occidentalis* (Marsh and Bennett, 1986*a,b*). Marsh and Bennett (1985) also described the force-velocity relationship of the IF muscle as a means for determining maximum power output and maximum shortening velocity (V_{\max}) of the muscle. Although the exact strain regimes are unknown, muscles involved in repetitive movements, such as running, will undergo cycles of shortening and lengthening. Estimates of power derived from force-velocity relationships deal only with force produced during shortening, and values so obtained represent an overestimate of power output available from a muscle undergoing cyclic length changes (Josephson, 1985, 1989). Muscle function during running is even more complicated because of stretch activation and shortening-induced deactivation (Josephson, 1985). These factors make it difficult to relate muscle function *in vivo* and isotonic/isometric contractile properties *in vitro*.

In order to mimic *in vivo* conditions more accurately when measuring muscle performance in relation to locomotor performance, we measured power output using the work-loop technique. Muscles were subjected to sinusoidal length changes and phasic stimulation while force and muscle length were measured. The area inside the loop formed on a force-position plot over a full length cycle is the difference between the work done during shortening (positive work) and the work required to restretch the muscle (negative work), or the net work done during that cycle (see Josephson, 1985). Using this technique, investigators have modelled power output during flight in insects (Josephson, 1985; Stevenson and Josephson, 1990), jumping in frogs (Stevens, 1988), swimming in fish (Altringham and Johnston, 1990*a,b*; Moon *et al.* 1991; Johnson and Johnston, 1991; Johnson *et al.* 1991) and respiratory movements in mammalian diaphragms (Syme and Stevens, 1989; Altringham and Young, 1991). However, the work-loop technique has not been used to correlate *in vitro* muscle function with locomotor performance in a terrestrial animal.

The present study tested the hypothesis of Marsh and Bennett (1985) that limb cycle frequency during burst running in lizards is limited by power output (i.e. contraction kinetics) of skeletal muscle at low body temperatures but not at higher temperatures.

Power output of the IF *in vitro* and whole-animal hindlimb cycling frequency were measured over a range of temperatures to allow comparison of the effects of temperature on the optimal cycling frequency *in vitro* and the achieved limb cycle frequency *in vivo*. A companion study (Johnson *et al.* 1993) examines the ontogenic size change in power output and burst speed in this lizard.

Materials and methods

Animals

Dipsosaurus dorsalis Hallowell were collected near Palm Springs, CA (California Scientific Collection Permit, AFB). Animals used for oscillatory work studies were collected in early spring and had a mean mass of 26.1 ± 5.6 g (\pm S.D., $N=11$). Animals used for analysis of hindlimb cycling frequency during burst running were collected in late June and weighed 28.2 ± 6.1 g (\pm S.D., $N=6$). The lizards were housed in temperature-controlled quarters with a 12h/12h light/dark cycle. They received food and water *ad libitum*.

Muscle preparation

Animals were anaesthetized using halothane vapour and killed by decapitation. The IF was isolated as described previously (Marsh and Bennett, 1985). The red portion and any damaged white fibres were removed, leaving a mass of white (fast glycolytic) fibres (30–50mg). One muscle was used immediately, while the contralateral muscle was maintained at room temperature overnight in oxygenated saline. The saline contained (in mmol l^{-1}): NaCl, 145; NaHCO_3 , 20; glucose, 11; KCl, 4; CaCl_2 , 2.5; MgCl_2 , 1; pH7.4 by bubbling with 95% O_2 :5% CO_2 . Preliminary experiments showed that muscle power output was not significantly different in those muscles stored overnight. The pelvis was anchored to a hook connected to a force transducer constructed from silicon strain gauges (Entran Sensors Inc., Fairfield NJ, USA). The transducer was mounted in the base of an experimental chamber. The distal tendon was connected to a Cambridge Instruments model 300H ergometer used to change muscle length. The muscle remained immersed in circulating saline in the chamber, with the temperature maintained at 15, 22, 35 or $42 \pm 0.1^\circ\text{C}$ using a heating/cooling coil. Force and length signals were amplified and displayed on a digital oscilloscope. Net work measurements were made by digital integration of the area inside the loop generated on a force–position plot.

Work-loop variables

Strain

The resting length of the muscle in the chamber was adjusted to give maximum isometric twitch tension without a significant increase in resting tension. Sinusoidal length changes about resting length were imposed on the muscle. The amplitude of the imposed length change, defined as muscle strain, was based on estimates of muscle length changes *in vivo* determined from video analysis of running animals. Using high-speed videotaping (see below), the hindleg positions of a running lizard were mapped. Muscle

length changes were then measured from partially dissected legs moved to the extreme positions reached by the limb during running. Total strain was found to be about 12%, expressed as a percentage of the muscle length at mid-stride. Therefore, in these experiments, strain was set at 12%; that is, the muscle length was varied from 94% to 106% of resting length. Josephson (1989) suggested that there is an inverse relationship between cycle frequency and the strain that gives maximal power output. However, we chose a constant strain at all frequencies since strain is related to stride length and stride length in this lizard has been shown to be relatively constant at cycle frequencies attained during running over the range of temperatures examined (Marsh and Bennett, 1985).

Stimulation

The muscle was stimulated *via* volume conduction through silver wires placed on either side of the muscle. A Grass stimulator was used to set the frequency and duration of stimulation. The current from the stimulator was amplified and passed through the silver wires. The pulse width, typically about 1ms, was adjusted to give the greatest isometric twitch tension for each temperature and each muscle preparation. The stimulation frequency used for tetanizing the muscle (60Hz at 15 and 22°C, 250Hz at 35 and 42°C) was the minimum rate that gave maximum isometric tetanic force.

Stimulus phase and duration

Work produced by a muscle depends not only on strain and cycle frequency, but also on the timing and duration of the stimulus burst. We use the term *phase* to refer to the point in the strain cycle at which stimulation begins. For each muscle preparation, cycle frequency and temperature, the phase and duration of stimulation were adjusted to maximise work output. The muscle was stimulated for four cycles in each experimental run. In all cases, work output stabilised by the third cycle, which was therefore selected for analysis. Experimental runs were performed at 10min intervals.

In vivo measurements

Limb cycling frequency during burst speed running was determined using high-speed videotaping. Animals were equilibrated in a temperature-controlled cabinet for at least 6h. Each lizard was chased down a 2m runway up to five times, while being videotaped at 400frames s⁻¹ (NAC high-speed video model HSV-400). The duration of each limb cycle was calculated and averaged for each animal at each temperature tested. Six animals were filmed at each of four temperatures (15, 22, 35 and 42°C). No fewer than four limb cycles were analyzed per animal per temperature.

Statistical analysis

A single-factor analysis of variance (one-way ANOVA; Sokal and Rohlf, 1981) was employed to determine whether temperature had a significant effect on the measured variables (Table 1). This was followed by a Scheffé test for multiple comparisons to isolate specific differences between the means at each temperature (Zar, 1974). A standard *t*-test was used to compare the optimal cycle frequency for the isolated preparations and the observed limb cycling frequency during burst running (Sokal and Rohlf, 1981).

Results

Twitch kinetics

The measured variables from isometric twitches at all experimental temperatures are summarised in Table 1. Both the time to peak tension (T_{PT}) and half-relaxation time ($R_{T1/2}$) are temperature dependent ($P < 0.001$, ANOVA) with significant differences between the means at each temperature ($P < 0.01$, Scheffé) except $R_{T1/2}$ between 35 and 42 °C. The results are very similar to those of Marsh and Bennett (1985). Both T_{PT} and $R_{T1/2}$ of the FG fibres of the IF have a Q_{10} of about 2.1 over the entire range of temperatures examined.

Oscillatory work

Net work output per cycle at optimum stimulus duration and phase decreases with increasing cycling frequency at all temperatures examined in this muscle (Fig. 1). Power (W), the product of the net work done by the muscle in a full cycle (J_{cycle}^{-1}) and the cycle frequency (cycles^{-1}), increases with increasing cycle frequency to a maximum and declines at higher frequencies (Fig. 2). The frequency at which power reaches a maximum, the optimal cycling frequency, increases significantly with temperature ($P < 0.001$, ANOVA), from 3.3 Hz at 15 °C to 20.1 Hz at 42 °C, with significant differences in the mean values at each temperature ($P < 0.01$, Scheffé; Fig. 3, Table 1). The frequency dependence of power output of the IF and the change in optimal cycling frequency with change in temperature are similar to findings for other muscles investigated with the work-loop approach (e.g. Syme and Stevens, 1989; Stevenson and Josephson, 1990; Johnson and Johnston, 1991).

Table 1. *The thermal dependence of the contractile properties of fast-twitch muscle fibres isolated from the iliofibularis of Dipsosaurus dorsalis*

	Temperature (°C)			
	15 (<i>N</i> =7)	22 (<i>N</i> =9)	35 (<i>N</i> =15)	42 (<i>N</i> =7)
T_{PT} (ms)	78.2 ± 2.6	* 38.8 ± 2.8	* 14.7 ± 0.8	* 11.1 ± 1.0
$R_{T1/2}$ (ms)	69.9 ± 3.8	* 28.6 ± 3.9	* 10.0 ± 0.8	10.1 ± 0.4
Limb cycling frequency (Hz)	2.6 ± 0.5	* 6.7 ± 0.3	* 10.7 ± 0.4	10.5 ± 0.6
Optimal cycling frequency (Hz)	3.3 ± 0.2	* 5.9 ± 0.3	* 17.1 ± 0.2	* 20.1 ± 0.9
Work per cycle ($J\text{kg}^{-1}$)	6.7 ± 0.6	7.6 ± 0.6	8.4 ± 0.5	7.8 ± 0.6
Power per cycle ($W\text{kg}^{-1}$)	19.6 ± 2.4	* 42.6 ± 2.3	* 143.9 ± 8.4	* 153.7 ± 0.4

Values are means ± S.E.

Asterisks separate values that are statistically significantly different ($P < 0.01$, Scheffé).

T_{PT} , time from onset of twitch to peak isometric tension.

$R_{T1/2}$, time from peak tension to 50% relaxation.

Limb cycling frequency is the frequency at which the hindlimb cycles during burst speed running.

Optimal cycling frequency is the cycling frequency at which the muscle produces maximum power *in vitro*.

Work and power values were obtained at the optimum cycling frequency for each muscle preparation.

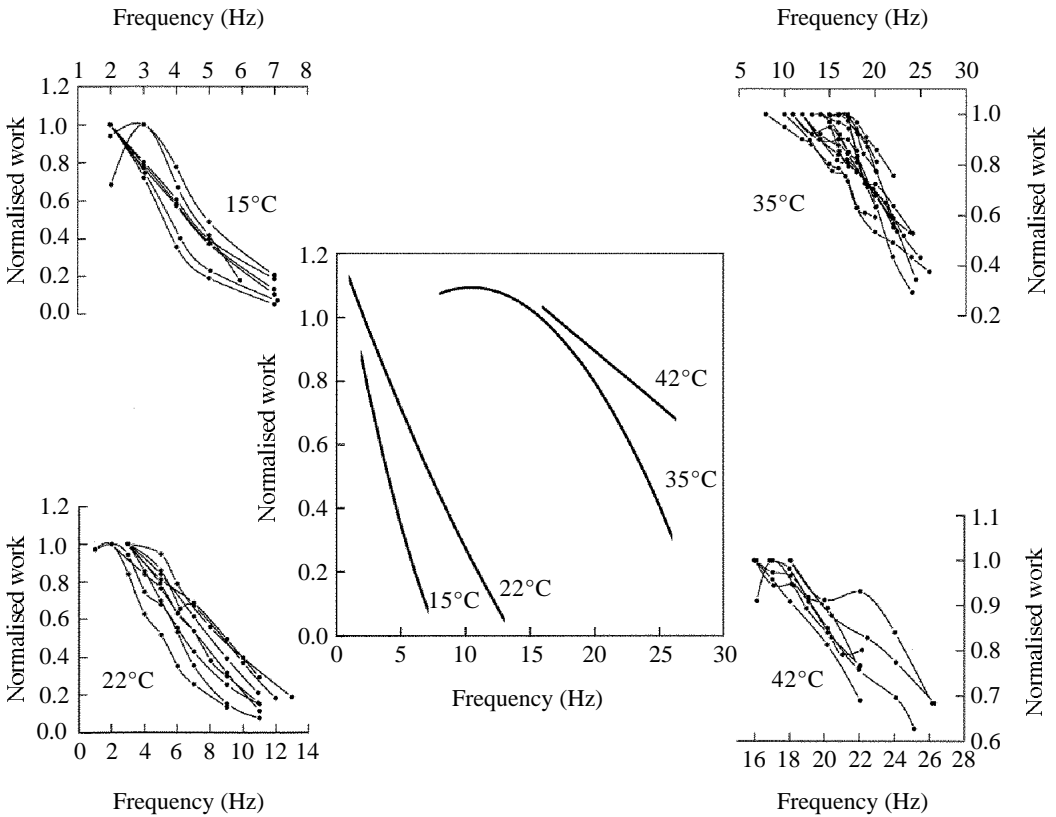


Fig. 1. Work done by the fast-twitch glycolytic fibres of the iliofibularis as a function of cycle frequency. Values are normalised to the maximum work for each preparation at each of the four temperatures (peripheral graphs). A spline curve is fitted to the data from each preparation using Sigmaplot 5.0 (Jandell Scientific). The central graph shows second-order polynomial regressions for all values obtained at each temperature; the relative vertical position of each curve is adjusted according to the mean work values shown in Table 1. (Normalised work at 22°C is equal to 1.0.)

Not only does temperature affect the optimal cycling frequency, but it also has a dramatic effect on the maximum power output of the IF ($P < 0.001$, ANOVA; Table 1). Maximum power output has a Q_{10} of 2.7 over the entire range of temperature, increasing from 20 W kg^{-1} at 15°C to 154 W kg^{-1} at 42°C . Because the net work output at the optimal cycling frequency is independent of temperature ($P > 0.05$, ANOVA; see Table 1), the thermal dependence of the power output (derived from net work and cycle frequency) comes principally from the thermal dependence of the optimal cycling frequency.

Isotonic vs sinusoidal shortening velocity

Although shortening velocity is continuously changing during sinusoidal length changes, an average shortening velocity can be determined using the cycle frequency and the strain imposed. The average shortening velocity that produces maximum power is expressed as \bar{V} at f_{opt} (i.e. at optimal cycling frequency; Fig. 4). Power measurements

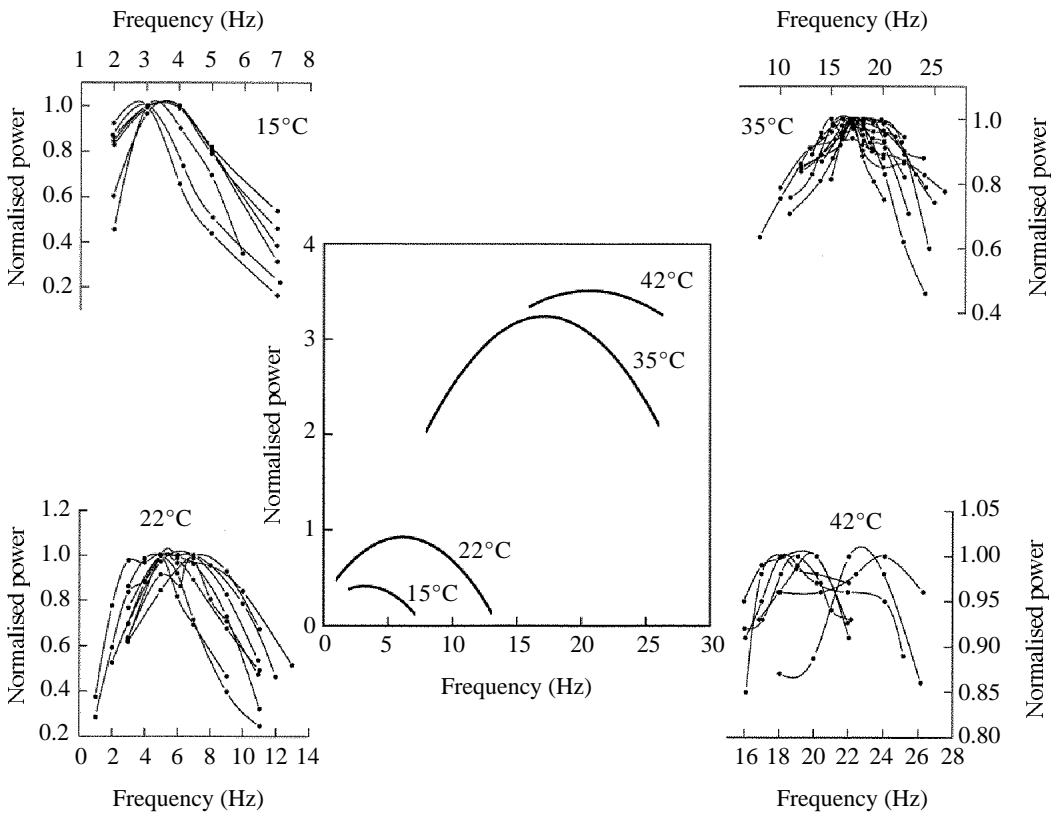


Fig. 2. Normalised power output as a function of cycle frequency. Data are presented as in Fig. 1.

from force–velocity curves, although an overestimate of power production *in vivo* (see above), represent the maximum attainable power and corresponding shortening velocity (V_{opt}) for the muscle. Using force–velocity values published for FG fibres of the IF (Marsh and Bennett, 1985), we calculated the shortening velocity for peak power (Fig. 4). The shortening velocity that produces peak power, as derived from force–velocity relationships, is the same average velocity employed for maximum power output during cyclic muscle length changes. Therefore, when hindlimb cycling frequency *in vivo* and optimal cycling frequency match (see below) at the *in vivo* strain fluctuations, the muscle is performing at an ‘optimal shortening velocity’ for power output.

Animal performance

Limb cycling frequencies during burst running also have a large thermal dependence with a Q_{10} of 2.5 in the temperature range of 15–35°C ($P < 0.001$, ANOVA; $P < 0.01$, Scheffé; Fig. 3, Table 1). The mean frequency is greatest at 35°C (10.7 Hz), with maximum frequency from individual animals varying from 9.0 to 12.5 Hz. The mean cycle frequency is similar to that reported by Marsh (1989) for animals in this size range (18–34 g). Increasing the temperature from 35°C to 42°C resulted in no change in stride

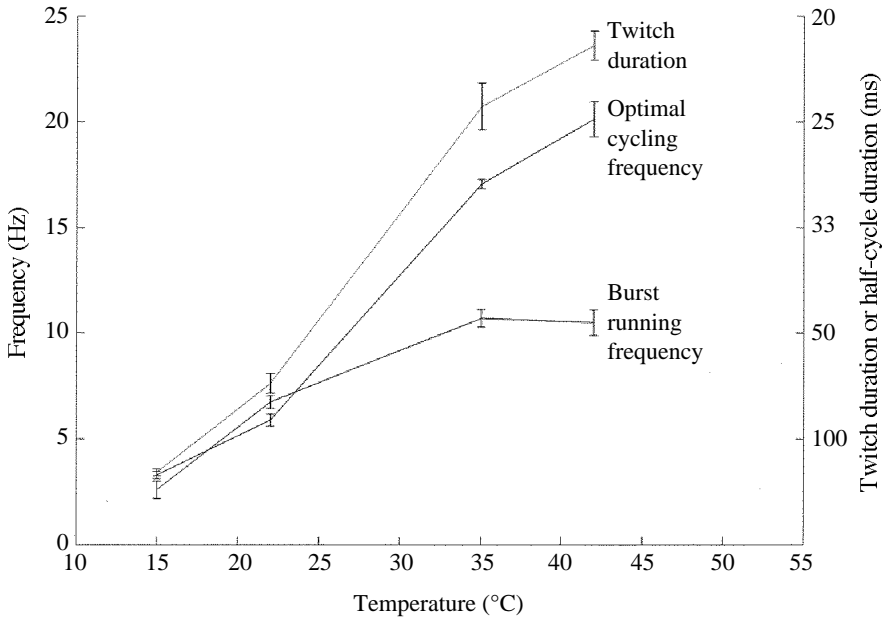


Fig. 3. The relationship between temperature and hindlimb cycling frequency measured during burst speed running, optimal cycle frequency for power output from isolated fast twitch fibres of the IF, and the duration of isometric twitches (time from onset to 50% relaxation). The values on the duration axis (right) correspond to the half-cycle time for frequencies on the opposing axis (left), e.g. at a cycle frequency of 10Hz, it takes 50ms to complete the shortening half of one full strain cycle. The twitch duration axis thus represents the time available to do shortening (positive) work at the corresponding cycle frequency on the opposing axis.

frequency (10.5 ± 0.6 Hz at 42°C , mean \pm S.E.; $P > 0.05$, Scheffé), in accordance with previous observations (Marsh and Bennett, 1985; Marsh, 1990).

Optimal cycling frequency vs burst stride frequency

At temperatures above 22°C , burst limb cycling frequency is significantly lower ($P < 0.01$, standard t -test) than the optimal cycling frequency for power output from the isolated muscle (Fig. 3, Table 1). For example, at 35°C , the hindlimb frequency during burst running is 10.7Hz while the isolated muscle preparation produces maximum power at 17.1Hz. However, at 15°C and 22°C , the burst cycling frequency and optimal cycling frequency are not significantly different ($P > 0.05$; Table 1).

Discussion

Twitch kinetics, work and optimal cycling frequency

The dramatic effects of temperature on contraction kinetics and work output are illustrated in Fig. 5, which compares twitches at several temperatures with the strain

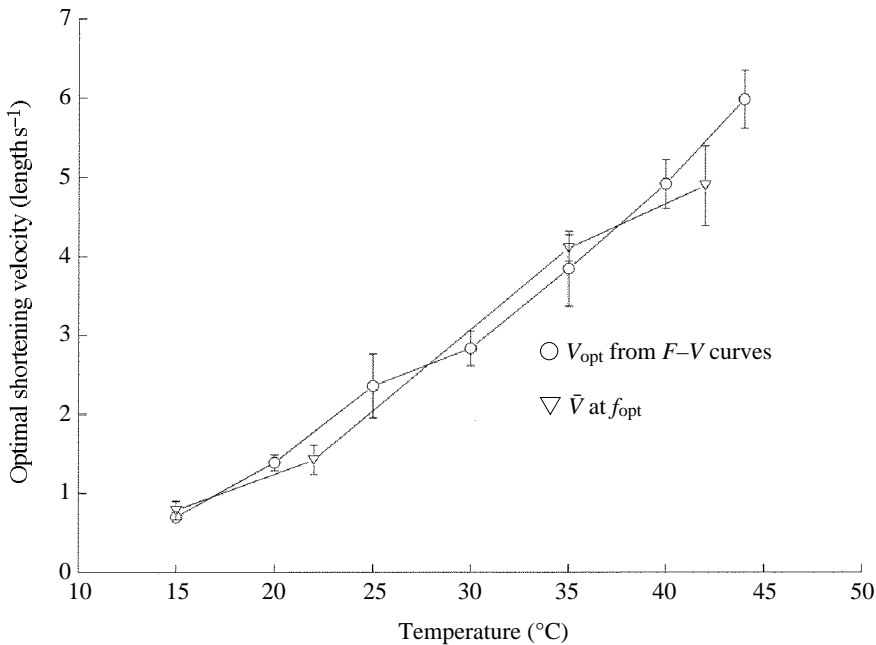


Fig. 4. Optimal shortening velocity, measured in different ways, as a function of temperature. V_{opt} , calculated from force–velocity values previously published (Marsh and Bennett, 1985), is the velocity of shortening that resulted in peak power production. \bar{V} at f_{opt} is the average velocity of shortening over a strain cycle at the optimal cycling frequency.

cycle that gives the greatest power output at 42°C (19Hz) and in Fig. 6, which compares work loops at several temperatures, all obtained at the cycle frequency at which power is maximal at 42°C. For maximal work output, the duration of muscle activation during a length cycle should be confined largely to the shortening phase of the cycle. Activation and high muscle force during the lengthening phase increase the work required to re-lengthen the muscle (negative work) and reduce the net work over a full cycle. Thus, the twitch duration becomes a limit on performance when it becomes longer than the shortening half-cycle. At 42°C, the duration of the isometric twitch is sufficiently short so that the entire twitch fits within the shortening phase of the cycle at 19Hz, which is the optimum frequency for power output at this temperature. As temperature is lowered, more and more of the twitch spills over into the lengthening phase and by 22°C the twitch duration easily spans two full strain cycles (Fig. 5).

During running at higher temperatures, it is likely that the FG fibres of the IF of *D. dorsalis* are activated in short, tetanic contractions rather than twitches (discussed in Marsh and Bennett, 1985). Clearly, during muscle sinusoids, stretch activation and shortening-induced deactivation (Josephson and Stokes, 1989) will allow short trains of stimuli, as opposed to single pulses, to be given without incurring increases in negative work. Certainly, maximum power output is achieved *in vitro* with a short, tetanizing burst of stimuli. The work loops of Fig. 6B (derived from force and length traces in Fig. 6A) were obtained using brief, tetanizing bursts of stimuli at 22, 35 and 42°C. The cycle

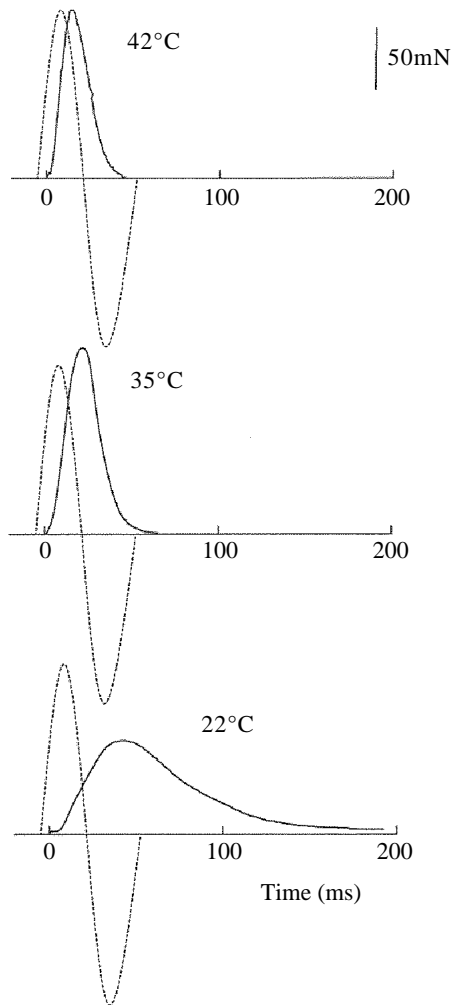


Fig. 5. Force records for isometric twitch contractions at 22, 35 and 42°C from a single representative preparation of FG fibres of the IF of *Dipsosaurus dorsalis*. Twitches (solid lines) are superimposed on a strain cycle of 19Hz (dashed lines), the cycle frequency at which power output was maximal at 42°C.

frequency was 19Hz and the strain was 12%. The muscle was stimulated in each case at the stimulus duration and phase that maximise net work output from the muscle at 42°C. The cycle frequency, phase and duration are therefore not optimal for power production at 22 and 35°C under these conditions. Clearly, the effects of temperature on both activation and relaxation time of the muscle during a short burst of stimuli dramatically affect the net work produced by the muscle. At the cycle frequency of 19Hz, the duration of muscle activation is too long at the lower temperatures to allow complete relaxation before lengthening begins, resulting in increased lengthening work and, at 35°C, a work

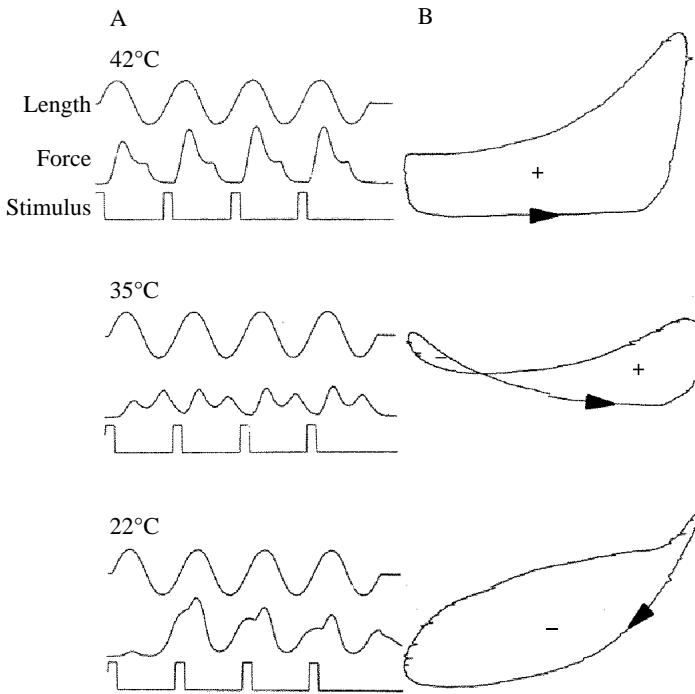


Fig. 6. (A) Force, length and stimulation records for a representative preparation of FG fibres performing oscillatory work at 22, 35 and 42°C at a 19Hz cycle frequency. Strain was set at 12%. The phase and duration of stimulation used at all three temperatures were those that maximised net work at 42°C. Both phase and duration remained unchanged for loops at 22 and 35°C to illustrate the effect of twitch duration on net work. These are therefore not optimal loops for the muscle at 22 and 35°C. (B) Corresponding work loops generated on force–position plots using the traces shown in A. A counterclockwise loop represents net work done by the muscle, whereas a clockwise loop represents net work done on the muscle.

loop with a clockwise portion (negative work) or, at 22°C, a work loop which is entirely negative (Fig. 6B).

Because net work is clearly affected by activation and relaxation, power production from a muscle must also be affected by the temperature-dependent kinetics of these processes. Maximum power production at each temperature occurs at frequencies that require short bursts of stimuli. However, with such short stimulus durations, the times of activation and relaxation take up a substantial part of the total time of tension production. Thus, these kinetics of activation and relaxation may play an important role in determining at which frequency maximum power occurs: they consume an increasing portion of the shortening half-cycle with increasing cycle frequency. Therefore, the relationship between isometric kinetics of the twitch and the cycle frequency which maximises power output (optimal cycling frequency) was examined. Fig. 3 demonstrates the relationship between twitch duration (time from onset to 50% relaxation) and optimal cycling frequency. For maximum net work, the duration of tension production should be

equal to and therefore considered in reference to, the half-cycle duration. The thermal dependence of the twitch duration and the shortening half-cycle duration at the optimal cycling frequency are similar (Fig. 3). Twitch duration measured from onset to 50% relaxation represents a good estimate of the cycle duration at which a muscle will produce maximum power using the work-loop technique.

Temperature, power output and locomotor activity

Marsh and Bennett (1985) suggested that twitch time-course limits limb cycling frequency at low temperatures but not at high temperatures in this lizard. We correlated the cycling frequency employed by the hindlimb during burst speed running and the cycling frequency that produced maximum power in isolated muscle preparations (optimal cycling frequency) over a range of temperatures. The cycle frequency at which the IF produces maximum power at 15 and 22°C matches very well the hindlimb frequency employed during burst running at these temperatures (Fig. 3, Table 1). Maximum power output from FG fibres therefore appears to limit the hindlimb cycling frequency at 15 and 22°C. Certainly, the animal could cycle its hindlimbs faster, but this would be at the expense of FG fibre power production and would possibly reduce speed.

At the higher temperatures of 35 and 42°C, the hindlimb cycling frequency reaches a plateau at 10–11 Hz (Fig. 3, Table 1). However, as a consequence of the faster contraction kinetics at these high temperatures, muscle power output from isolated preparations is maximal at frequencies much higher (17 and 20 Hz at 35°C and 42°C, respectively) than the hindlimb cycling frequency (Fig. 3; see also Fig. 3 of Johnson *et al.* 1993). Presumably, the muscle is working below its full potential for power production *in vivo* at these temperatures. For example, at 35°C, the average power produced by the isolated muscle when cycling at the measured hindlimb cycling frequency (11 Hz) was $60.1 \pm 3.6 \text{ W kg}^{-1}$ (S.E., $N=15$), while 144 W kg^{-1} would have been available if the muscle had operated at 17 Hz. Thus, above 22°C contractile events no longer limit the frequency at which the hindlimb can cycle. The reasons why the animal operates at frequencies less than those required for maximum power from the IF remain unclear (discussed in Johnson *et al.* 1993).

Estimates of power obtained using the work-loop technique were about half the value of peak power estimated from force–velocity curves (Marsh and Bennett, 1985). This observation reconfirms the expectation that measurements of muscle power output from force–velocity curves overestimate power output available *in vivo* from a cycling muscle (Josephson, 1989). To date, the power output of the IF at 42°C, 154 W kg^{-1} , is the highest recorded power output obtained with the work-loop technique.

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