

## Thermal Dependence of Isometric Contractile Properties of Lizard Muscle

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**Summary.** 1. The thermal dependence of the isometric contractile properties of the iliofibularis and gastrocnemius muscles were studied at 5 °C intervals from 10–50 °C in lizards with different preferred body temperatures (PBT): *Dipsosaurus dorsalis* (PBT: 40–42 °C); *Cnemidophorus murinus* (40 °C); *Sceloporus occidentalis* (35 °C); and *Gerrhonotus multicarinatus* (25–30 °C).

2. Isometric twitch and tetanic tensions were constant over a broad temperature range (as much as 25 °C) in all species. Tetanic tension declined by 50% at 45–47.5 °C in *Dipsosaurus*, 42.5 °C in *Cnemidophorus*, and 40 °C in *Sceloporus* and *Gerrhonotus*.

3. Twitch contraction time (CT—the time to the peak twitch tension) increased with decreasing temperature from 10 ms to 300 ms. At any given temperature, the muscles of *Sceloporus* and *Gerrhonotus* had faster CTs than those of the other species. The CTs were minimal at the maximal test temperature.

4. The maximal rate of tension development with tetanic stimulation ( $dP_0/dt$ ) was strongly temperature dependent and was maximal at 40–45 °C in *Dipsosaurus*, 40–42.5 °C in *Cnemidophorus*, and 35 °C in *Sceloporus* and *Gerrhonotus*.

5. The time properties of these muscles are highly temperature dependent and contractile tensions are broadly temperature independent. Except in *Gerrhonotus* muscles, the combination of twitch speed and tension generating capability is maximal at PBT, although neither parameter alone is maximized at PBT.

the understanding of the role that muscle plays in linking physiology and behavior. Considering this importance, there are surprisingly few studies on the effects of temperature on muscle performance. The muscles of lizards are particularly well suited for such a study. Most lizard species are voluntarily active over a wide range of body temperatures but preferentially function at a single temperature (preferred body temperature – PBT). The thermal dependence of activity (Bennett 1980) and several physiological systems (for review see Dawson 1975) have been studied in many lizard species. However, there are only two studies of the thermal dependence of lizard muscle performance (Licht 1964; Licht et al. 1969) and these deal only with twitch tension.

We have undertaken a study to determine the thermal dependencies of several isometric parameters including twitch tension ( $P_1$ ), tetanic tension ( $P_0$ ), twitch contraction time (CT), twitch 1/2 relaxation time (1/2 RT) and the maximal rate of tension rise during a tetanus ( $dP_0/dt$ ). Such a spectrum of measurements is necessary to determine the thermal dependencies of both rate functions (CT, 1/2 RT,  $dP_0/dt$ ) and capacity functions ( $P_1$ ,  $P_0$ ) and thus to describe fully the effects of temperature on isometric contractions.

Four species of lizards with different PBT were selected for this study: *Dipsosaurus dorsalis*, PBT of 40–42 °C (Norris 1953); *Cnemidophorus murinus*, PBT of 40 °C (Bennett and Gorman 1979); *Sceloporus occidentalis*, PBT of 35 °C (Brattstrom 1965); and *Gerrhonotus multicarinatus*, PBT of 25–30 °C (Brattstrom 1965; Licht 1964). The purpose of this experiment was to determine the thermal dependence of the isometric properties of muscles of four lizard species having different PBTs, and to correlate these properties with PBT. A preliminary report of this work has been made previously (Putnam and Bennett 1981).

### Introduction

An understanding of the effect of temperature on muscle performance has important implications for

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**Abbreviations:** CT twitch contraction time; CTM critical thermal maximum; IF iliofibularis muscle; PBT preferred body temperature;  $P_0$  tetanic tension;  $P_1$  twitch tension; 1/2 RT twitch half relaxation time

### Materials and Methods

**Animal Collection and Maintenance.** *Dipsosaurus* ( $n=7$ , mass  $\pm$  SE = 49.1  $\pm$  1.7 g), *Sceloporus* ( $n=6$ , mass = 11.4  $\pm$  1.6 g), and *Ger-*

*rhonotus* ( $n=5$ , mass =  $25.4 \pm 2.4$  g) were collected locally in southern California and maintained in the laboratory less than 2 months before experimentation (6 months for *Gerrhonotus*). *Cnemidophorus* ( $n=3$ , mass =  $58.4 \pm 2.8$  g) were collected on the island of Bonaire, Netherlands Antilles and returned to the University of California where they were kept in the laboratory. Lizards were maintained in terraria (at 25 °C) equipped with incandescent lights to permit thermoregulation with a 12:12 light:dark cycle centered on noon. Lizards were fed two or three times per week with mealworms (*Tenebrio* larvae) (*Gerrhonotus*, *Sceloporus*, *Dipsosaurus*) or dog-food and lettuce (*Cnemidophorus*, *Dipsosaurus*). *Dipsosaurus* were also fed the flowers of the common butterweed (*Senecia* sp.). Experiments were performed in the late fall and early winter.

Lizards were sacrificed by decapitation and the skin from both hind limbs removed. The distal tendon of the iliofibularis (IF) muscle was tied with 00 surgical silk and the muscle dissected free. The IF muscle was then removed with a portion of the pelvic bone. The gastrocnemius muscle was tied at the Achilles tendon, dissected free, and removed from the animal with a portion of the femur. The IF and gastrocnemius muscles from both limbs were removed. During dissection and after removal, the muscles were bathed in a Ringer solution oxygenated with 95% O<sub>2</sub> and 5% CO<sub>2</sub>. The Ringer solution contained 145 mM NaCl, 4 mM KCl, 20 mM imidazole and 2 mM CaCl<sub>2</sub>. The pH of this solution varied randomly with temperature between 7.25 and 7.40.

**Experimental Apparatus.** The bone attached to a muscle was held by a clamp in a plexiglas base. A hollow plexiglas cylinder (height: 7.2 cm, internal diameter: 3.1 cm), with inlet and outlet ports for Ringer solution, was lowered over the muscle and fit into the base to make a water-tight bathing chamber. The thread was tied to a light metal chain and suspended from a Grass FT03.C force transducer. The transducer was held by a micromanipulator to allow for fine adjustment of muscle length. The compliance of the transducer and its support were reduced by placing a rigid metal bar directly under the distal portion of the transducer. This bar was held in place by attaching it to a magnetic base. Ringer solution was circulated from a 1 liter reservoir through the chamber with a peristaltic pump. The Ringer solution was lightly bubbled with 95% O<sub>2</sub> and 5% CO<sub>2</sub> through PE 10 tygon tubing placed in the chamber. The temperature of the Ringer solution was controlled by circulating it through several coils of tygon tubing in either an ice bath or hot water bath before entering the muscle chamber. This arrangement allowed for temperatures to be changed by 5 °C within 2–3 min and to be maintained at  $\pm 0.5$  °C. Temperature was monitored with a Markson Digital Thermometer with a calibrated flexible probe placed in the bathing chamber close to the muscle. Stimulation was delivered from a Grass SD5 Stimulator through two S-shaped platinum surface electrodes. The electrodes were placed so that current passed diagonally through the muscle. Stimulus intensity varied from 20–100 V and was 1 ms in duration. Tetanic stimulation was at a frequency of 150–200 Hz above 35 °C, 120 Hz at 30 °C and 100 Hz at 25 °C and below for *Dipsosaurus* and *Cnemidophorus* muscles. For *Sceloporus* and *Gerrhonotus* muscles, tetanic stimulation frequency was 200 Hz above 25 °C and 120 Hz from 10–20 °C. These frequencies were selected to assure fused tetani and maximal tetanic tension.

The output of the force transducer was fed to a 741 operational amplifier with a gain of 1,000. The output of the amplifier was displayed on a Tektronix 5111 Storage Oscilloscope. Data were collected directly from the oscilloscope trace and also photographed with a C5C Polaroid camera for later analysis. The output of the amplifier was also fed to a differentiating circuit constructed from a 741 operational amplifier with a time constant of 0.1 s. The 90% response time of the entire system was 4 ms.

**Experimental Protocol.** A standard protocol was followed for all muscles. A series of twitches were delivered initially and muscle

length was adjusted to yield maximal isometric twitch tension. Muscle temperature was then raised to the initial test temperature (40 °C in *Dipsosaurus* and *Cnemidophorus*, 35 °C for *Sceloporus* and *Gerrhonotus*). The muscles were allowed 15 min to equilibrate and were given a series of 2 to 3 twitches. This stimulation was followed by an isometric tetanus of 500 ms duration; longer tetani were required at very low temperatures. This procedure was repeated as muscle temperature was lowered at 5 °C intervals down to 10 °C, with a 5 min equilibration period at each temperature. The muscles were returned to the initial test temperature and allowed 15 min to equilibrate. Twitch and tetanic parameters were re-measured to determine the degree of muscle fatigue. There was an average loss of 16% of initial tension due to the experimental procedure. The muscle was then heated at 2.5–5 °C intervals (with a 5 min equilibration period) until contractile responses were lost. Several muscles were cooled and re-tested to verify that this heat damage was irreversible. At the end of the experiment, muscle length was measured with Vernier calipers. The muscle was removed from the chamber, the bone and tendons dissected away, and the muscle was blotted and weighed to the nearest 0.1 mg. Cross sectional area was calculated by dividing the mass of the muscle (gastrocnemius:  $444 \pm 33$  mg in *Dipsosaurus*,  $429 \pm 22$  mg in *Cnemidophorus*;  $54 \pm 7$  mg in *Sceloporus*,  $35 \pm 2$  mg in *Gerrhonotus*; IF:  $119 \pm 8$  mg in *Dipsosaurus*,  $197 \pm 17$  mg in *Cnemidophorus*,  $28 \pm 6$  mg in *Sceloporus*,  $12 \pm 1$  mg in *Gerrhonotus*) by the muscle length (gastrocnemius:  $2.3 \pm 0.1$  cm in *Dipsosaurus* and *Cnemidophorus*,  $1.3 \pm 0.1$  cm in *Sceloporus*,  $1.2 \pm 0.1$  cm in *Gerrhonotus*; IF:  $2.3 \pm 0.2$  cm in *Dipsosaurus*,  $2.1 \pm 0.3$  cm in *Cnemidophorus*,  $1.4 \pm 0.1$  cm in *Sceloporus* and *Gerrhonotus*). By calculating cross-sectional area in this manner, we underestimate the area of the pinnate gastrocnemius muscle compared to the parallel-fiber IF muscle, accounting for a portion of the difference in absolute tension measured in these two muscles. All muscle tensions are expressed as Newtons per square meter of cross-sectional area (N/m<sup>2</sup>). After each experiment, the transducer was calibrated by hanging weights from it.

Twitch and tetanic tensions were obtained at each temperature for all muscles. In addition, twitch contraction time (CT – the time from the initiation of a contractile response to the maximal twitch tension) and the 1/2 relaxation time (1/2 RT – the time from the maximal twitch tension to 1/2 of this value during relaxation) were measured. Finally, the maximal rate of tension generation during a tetanus ( $dP_0/dt$ ) was obtained from the output of the differentiator.

All values are given as the mean  $\pm 1$  standard error of the mean (SE).

## Results

A composite oscilloscope tracing of twitch tensions at different temperatures for a gastrocnemius muscle from *Dipsosaurus* is shown in Fig. 1. Twitch tension and duration increase with decreasing temperature down to 15 °C. The effects of temperature on isometric twitch tension in both muscles for the four species are shown in Figs. 2 and 3. The tensions are normalized to the maximal twitch tension for each muscle to permit interspecific comparisons. Absolute tension at any temperature may be calculated with the maximal twitch tensions, which are reported in Table 1. Individual muscles may achieve maximal twitch tension at temperatures as low as 10 °C (Figs. 2 and

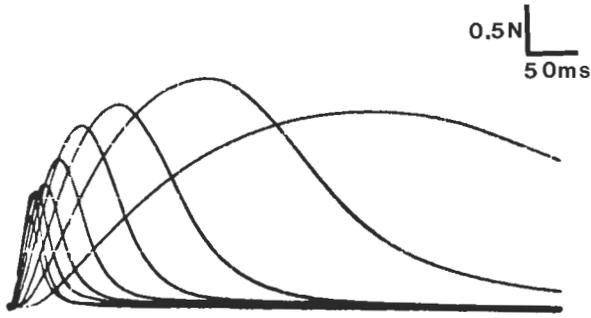


Fig. 1. Oscilloscope tracing of twitches at various temperatures in *Dipsosaurus* gastrocnemius muscle. From left to right: twitches are at 47.5, 45, 40, 35, 30, 25, 20, 15, and 10 °C

3). Thus twitch tension may remain high even at low body temperatures. The twitch tensions of the muscles of *Cnemidophorus* are more cold sensitive than the other species (Figs. 2 and 3, Table 1). The sensitivity to high temperatures correlates well with preferred body temperature of each species and with critical thermal maximum (CTM) (Table 1, Figs. 2 and 3).

Tetanic tensions are reported in Figs. 4 and 5 and

Table 1. These are more temperature dependent than are twitch tensions; however, most muscles are able to generate over 80% maximal tetanic tension over a 15 °C range (Table 1). In contrast to twitch tension, the tetanic tensions of all muscles are sensitive to cold temperature (i.e., 10–15 °C) and are clearly maximized at higher temperatures (Figs. 4 and 5). At very high temperatures, the loss of tetanic tension is similar to the loss of twitch tension and is similarly correlated with PBT and CTM of each species (Table 1). The experimental exposure to progressively colder temperatures and then re-testing at initial test temperature resulted in an average of 16% loss of tension (maximum of 30%). A further loss of tension at very high temperatures is due to irreversible heat damage. The upper thermal tolerance of the muscles varies among species and is in excess of the high temperature limit of the intact organism (Figs. 2 and 3, Table 1).

The relative changes in twitch and tetanic tensions are indicated by the twitch/tetanus ratio ( $P_t/P_0$ ) and shown for lizard muscles in Fig. 6. With decreasing temperature (below 25 °C)  $P_t/P_0$  increases from around 0.3 to 0.4 at 25 °C up to 0.8 at 10 °C. From

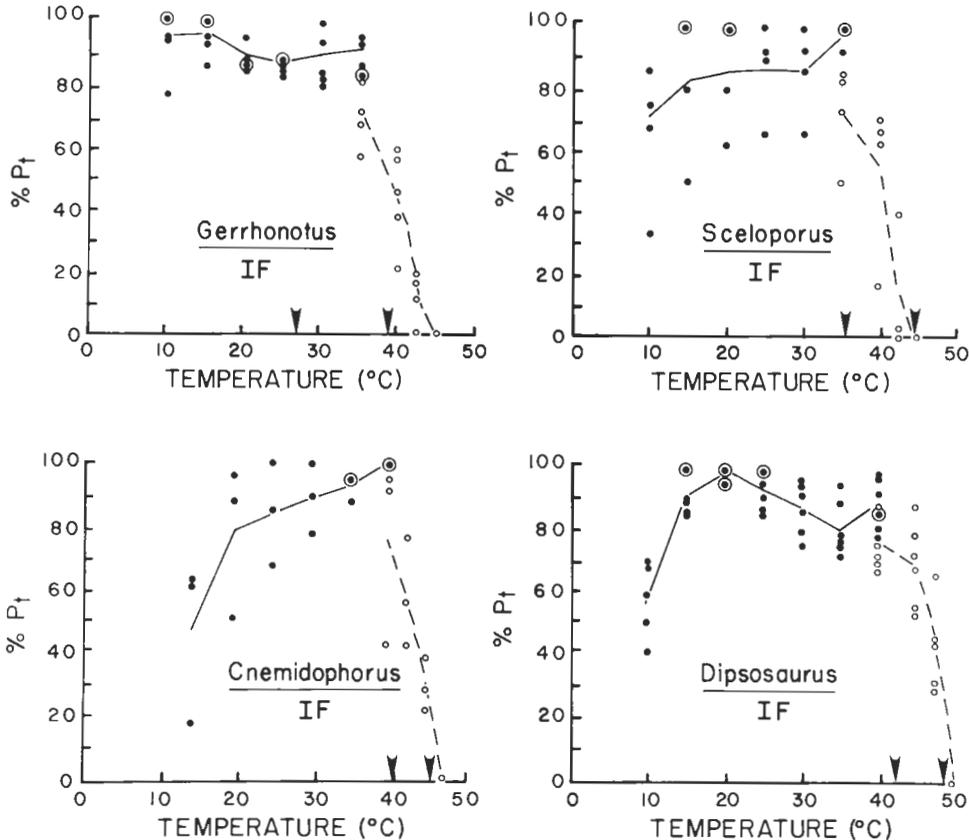


Fig. 2. Isometric twitch tension ( $P_t$ ) in IF muscles as a function of temperature. Each point represents tension for 1 muscle during descending (filled circles) or ascending (open circles) temperature series. Solid and dashed lines connect mean tension for a given temperature. On the temperature axis, arrow at lower temperature represents PBT, arrow at higher temperature represents CTM for a species (from Licht 1964; Bennett 1980). Circled points represent 2 or more points

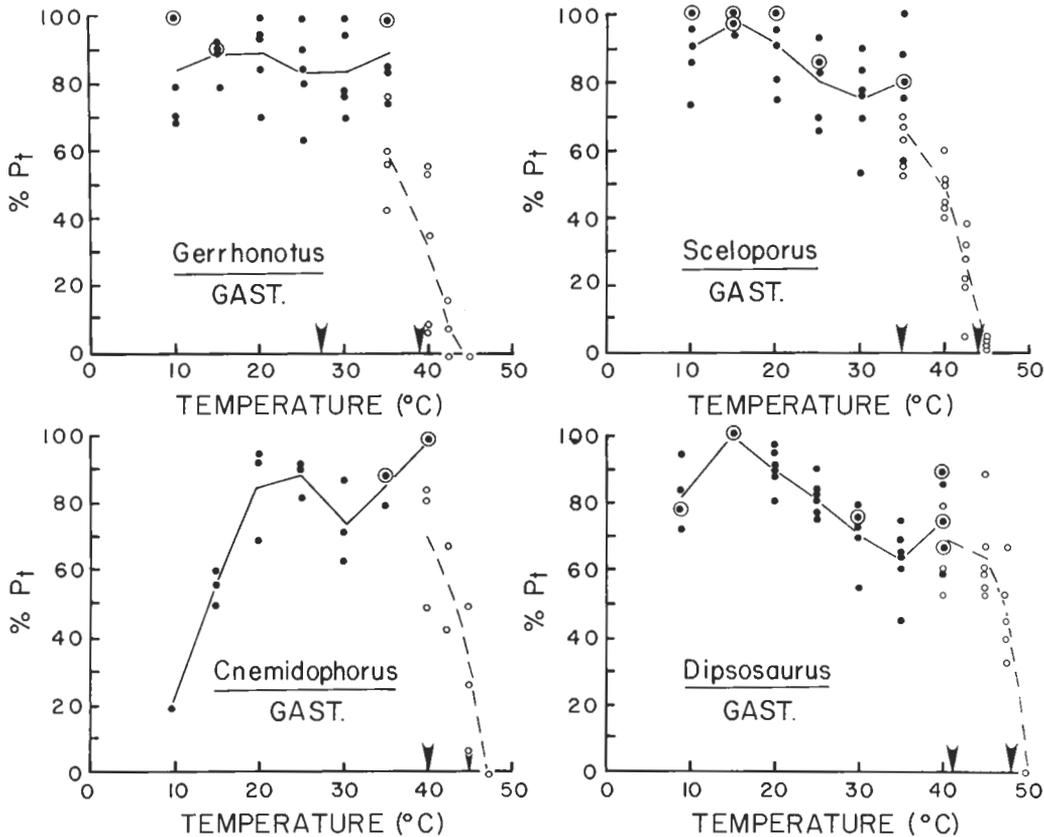


Fig. 3. Isometric twitch tension ( $P_t$ ) in lizard gastrocnemius muscle as a function of temperature. All symbols as in Fig. 2

Table 1. Maximal twitch and tetanic tensions, the temperature range for maximal performance ( $>80\% P_{max}$ ) and the upper temperature limit ( $<20\% P_{max}$ )

| Species<br>(PBT/CTM in °C)       | Gastrocnemius | Iliofibularis                   |                     |                     |                                 |                     |                     |
|----------------------------------|---------------|---------------------------------|---------------------|---------------------|---------------------------------|---------------------|---------------------|
|                                  |               | Tension<br>(kN/m <sup>2</sup> ) | $T_{>80\%}$<br>(°C) | $T_{<20\%}$<br>(°C) | Tension<br>(kN/m <sup>2</sup> ) | $T_{>80\%}$<br>(°C) | $T_{<20\%}$<br>(°C) |
| <i>Dipsosaurus</i><br>(40–42/48) | Twitch        | 114 ± 8                         | 10–25               | 50                  | 78 ± 8                          | 15–40               | 50                  |
|                                  | Tetanus       | 262 ± 23                        | 20–40               | 50                  | 178 ± 10                        | 25–40               | 50                  |
| <i>Cnemidophorus</i><br>(40/45)  | Twitch        | 90 ± 6                          | 20–40               | 47.5                | 72 ± 11                         | 25–40               | 47.5                |
|                                  | Tetanus       | 182 ± 11                        | 25–40               | 47.5                | 137 ± 23                        | 25–40               | 50                  |
| <i>Sceloporus</i><br>(35/44)     | Twitch        | 103 ± 8                         | 10–25               | 45                  | 48 ± 13                         | 15–35               | 42.5                |
|                                  | Tetanus       | 237 ± 18                        | 20–35               | 42.5                | 85 ± 21                         | 20–35               | 42.5                |
| <i>Gerrhonotus</i><br>(25–30/39) | Twitch        | 79 ± 14                         | 10–35               | 42.5                | 48 ± 24                         | 10–35               | 42.5                |
|                                  | Tetanus       | 237 ± 51                        | 20–35               | 42.5                | 135 ± 4                         | 20–35               | 42.5                |

25 °C to 35–40 °C,  $P_t/P_0$  is fairly constant and then increases to about 0.6 above 40 °C.

Both twitch CT and 1/2 RT are highly thermally dependent, decreasing with increasing temperatures in all muscles (Fig. 7). Twitches are fastest at the highest test temperature for each muscle. The shapes of the curves for CT and 1/2 RT vs temperature are similar among the 4 species, although the curves of the less thermophilic species (*Sceloporus*, *Gerrhonotus*)

are situated to the left. At any given temperature, these species have faster twitches than do *Cnemidophorus* and *Dipsosaurus* (Fig. 7). The similarity of the thermal dependence of the twitch of all muscles is shown by the similarity in the temperature coefficients ( $Q_{10}$ ) of the muscles of the 4 species over any given temperature range (Table 2).

The maximal rate of tension development during a tetanus ( $dP_0/dt$ ) can be used as an indicator of

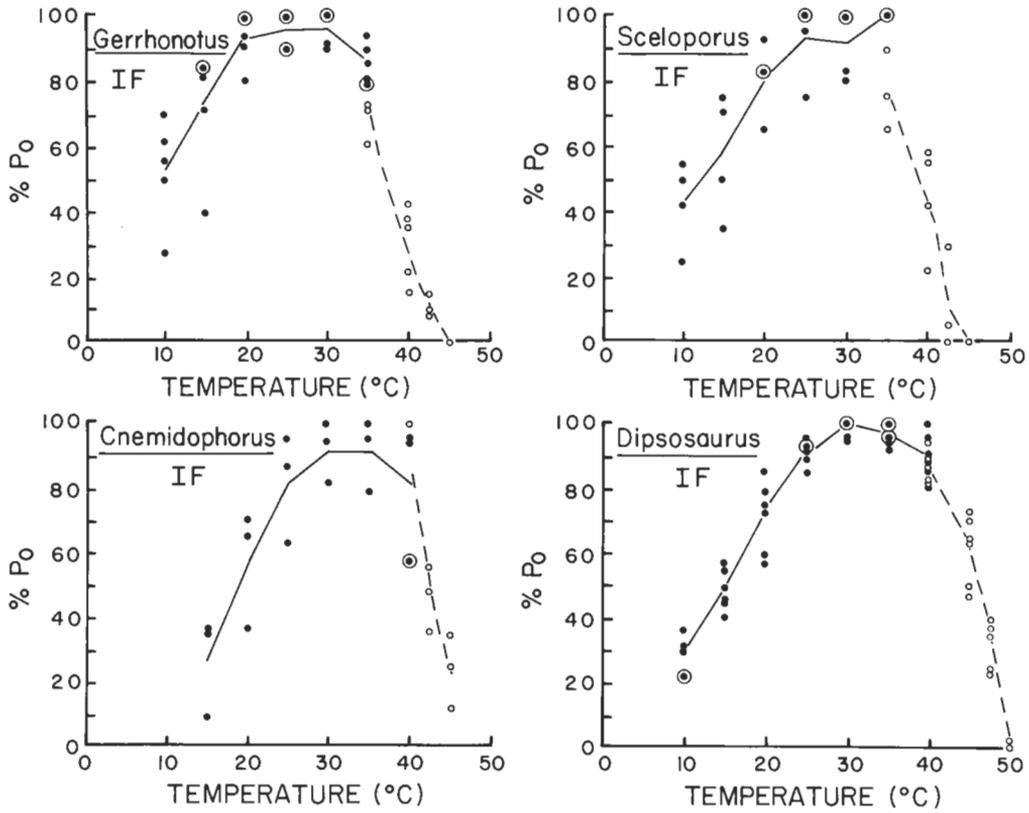


Fig. 4. Isometric tetanic tension ( $P_0$ ) in lizard IF muscle as a function of temperature. All symbols as in Fig. 2

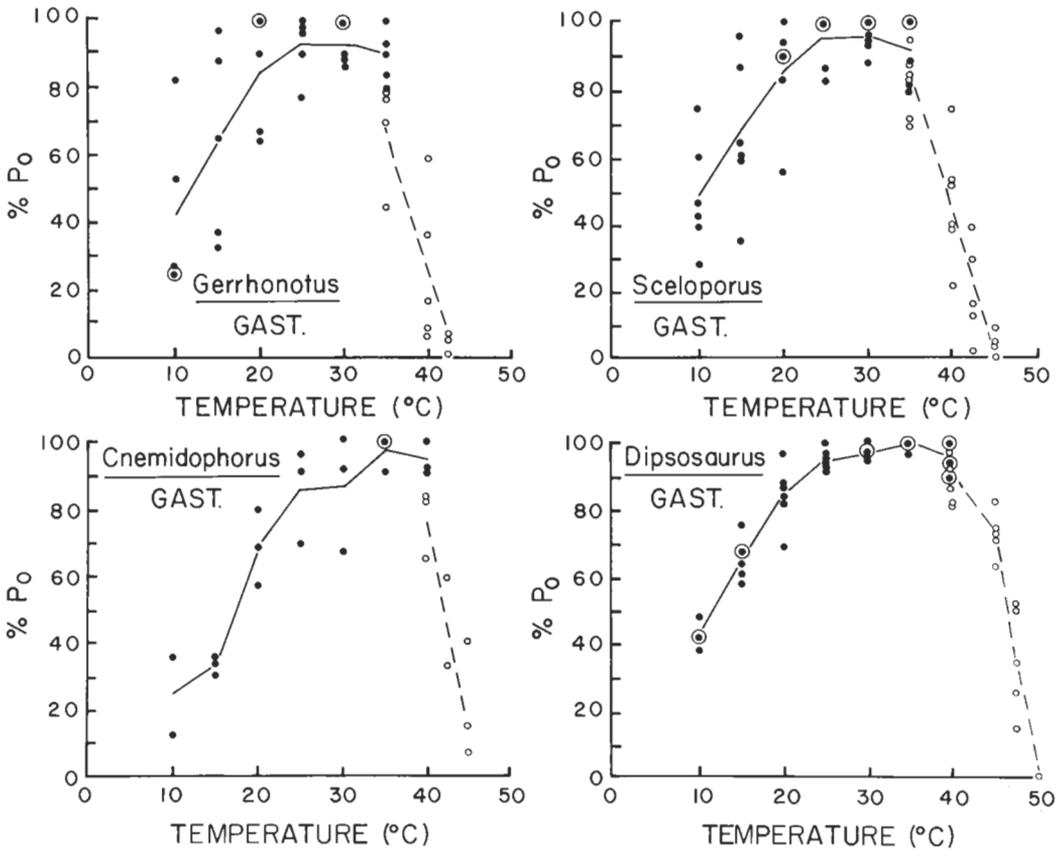


Fig. 5. Isometric tetanic tension ( $P_0$ ) in lizard gastrocnemius muscle as a function of temperature. All symbols as in Fig. 2

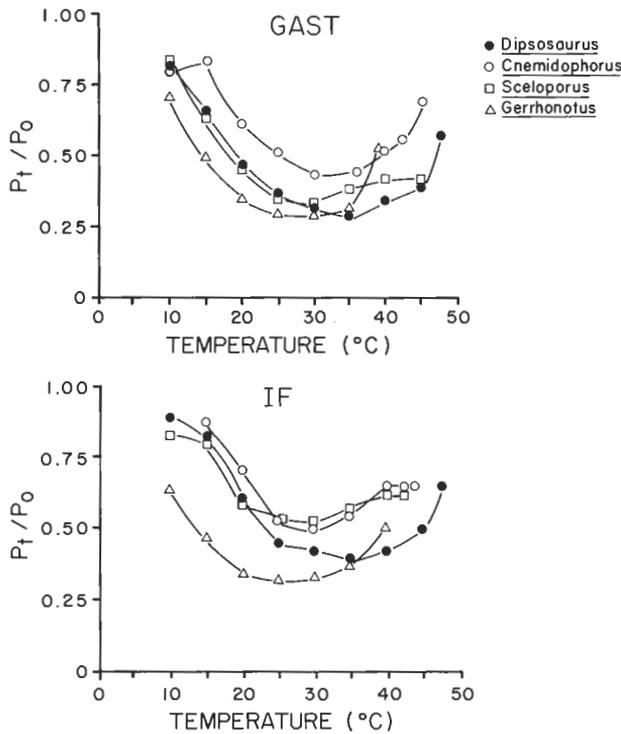


Fig. 6. Twitch/tetanus ratio ( $P_t/P_0$ ) as a function of temperature in lizard gastrocnemius and IF muscles. Points represent mean  $P_t/P_0$  for a species at a given temperature

the optimization of both contractile speed and tension. This parameter has a high thermal dependence in the muscles of all species, decreasing sharply at both high and low temperatures (Fig. 8). The  $dP_0/dt$  is maximal at 40–45°C in *Dipsosaurus*, 40–42.5°C in *Cnemidophorus* and at 35°C in *Sceloporus* and *Gerrhonotus*. Thus, with the exception of *Gerrhonotus*, the maximal value of  $dP_0/dt$  occurs at PBT.

The temperature coefficients ( $Q_{10}$ ) for the 5 isometric parameters are given in Table 2. For the 3 rate parameters (CT, 1/2 RT,  $dP_0/dt$ ) the coefficient used is the standard  $Q_{10}$ . Since no theoretical temperature coefficient exists for capacity parameters, the equation for  $Q_{10}$  was used to calculate temperature coefficients for the capacity parameters ( $P_t$  and  $P_0$ ). This allows direct comparison of the thermal dependence of all isometric parameters. The  $Q_{10}$  varied among the isometric parameters, showing clearly that there is no unified temperature effect on all the isometric properties of lizard muscle.

## Discussion

Each aspect of isometric contraction of lizard skeletal muscle has a different thermal dependence. Twitch

and tetanic tensions are broadly temperature independent, although twitch tensions remain maximal at lower temperatures than do tetanic tensions. Twitch kinetic parameters (contraction and 1/2 relaxation times) decrease with increasing temperature in all species up to the highest temperatures tested. In contrast to both of these previous patterns, the maximal rates of tension rise during a tetanus ( $dP_0/dt$ ) are strongly temperature dependent and attain maximal values at intermediate temperatures, generally at PBT (except in *Gerrhonotus*). No uniform pattern of thermal dependence underlies all these aspects of muscle function and no similar optimality is achieved at any individual temperature.

These patterns of thermal dependence are in general agreement with previous studies on the thermal dependence of isometric muscle performance in a variety of organisms. They conflict, however, with the studies of Licht (1964) and Licht et al. (1969) on the thermal dependence of twitch tension in the muscles of various lizard species, including some of the same species examined in this study. Licht (1964) and Licht et al. (1969) reported that twitch tensions are maximal at high temperatures, close to the PBT of the organism. Their results are more similar to our data on tetanic tension than twitch tension. This discrepancy may be related to their stimulation regime. Since stimulus duration was supermaximal in the studies of Licht (1964) and Licht et al. (1969), their results may represent tensions from partially or fully fused tetani rather than individual twitches.

Temperature can affect twitch tension in a variety of ways. Increasing temperature will increase the activity of myofibrillar ATPase (mATPase) and thus increase the maximum velocity of shortening ( $V_{max}$ ) of the contractile component (Bárány 1967). Marsh and Bennett (1981) have recently demonstrated an increase in  $V_{max}$  with increasing temperature in lizard muscles. This increase in  $V_{max}$  should lead to an increase in twitch tension (Josephson 1981). However, increasing temperature will also shorten the duration of the active state (Josephson 1981), resulting in a decrease in twitch tension. Indeed, even fast twitch muscles may not be fully activated by a single twitch at high temperatures (Ranatunga 1977). High temperatures can also lead to irreversible damage to the muscle and thus reduce the capacity to generate tension. Therefore, the thermal dependence of a muscle twitch reflects a compromise of the thermal dependence of a number of different processes. In certain flight muscles (Buchthal et al. 1957; Josephson 1981) and singing muscles of insects (Josephson 1981), twitch tension increases with increasing temperature. In contrast, the twitch tensions of frog (Hill 1951) and rat fast muscle (Close and Hoh 1968) decrease

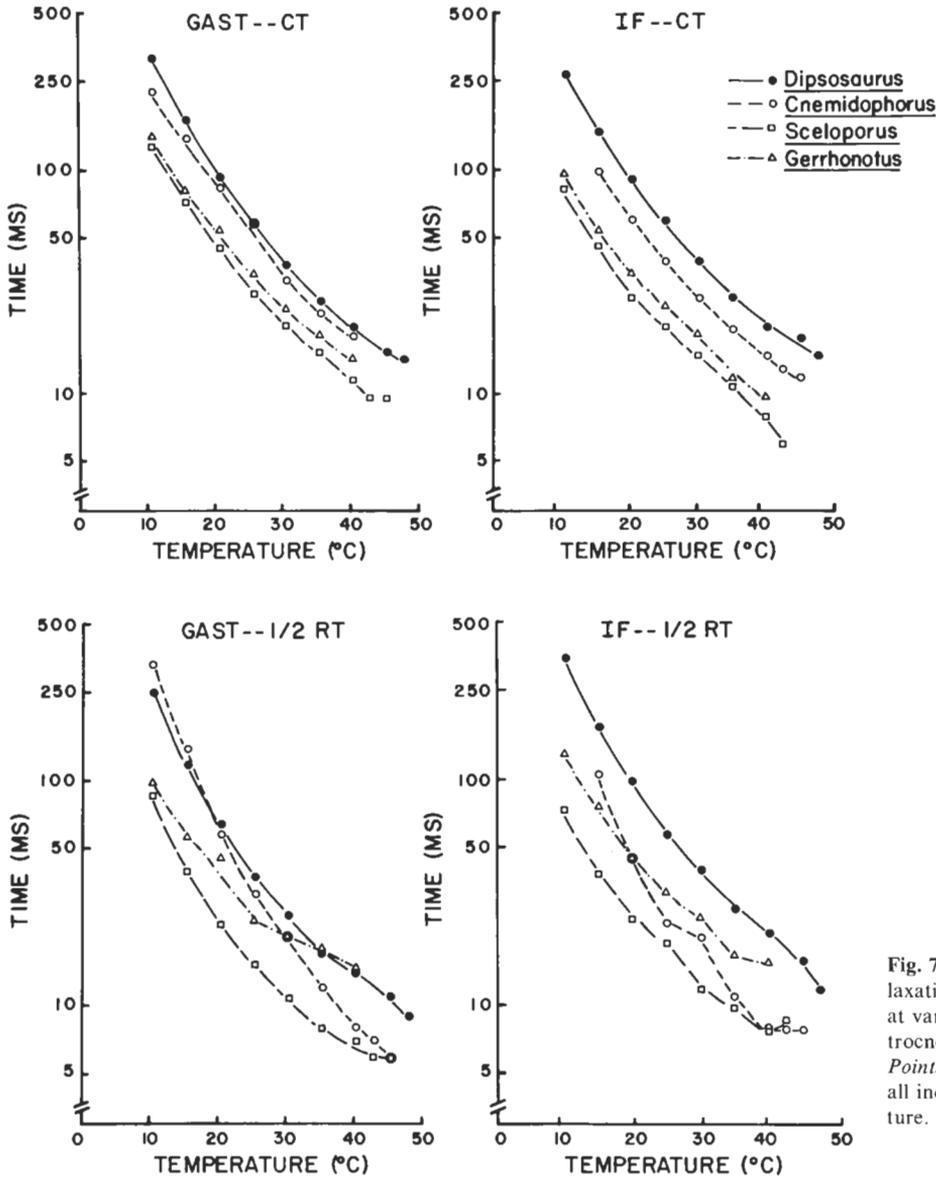


Fig. 7. Contraction time (CT) and 1/2 relaxation time (1/2 RT) of isometric twitches at various temperatures in the IF and gastrocnemius muscles of 4 species of lizards. Points represent mean CT and 1/2 RT of all individuals of a species at that temperature. Note the plots are semilogarithmic

with increasing temperature. The lizard muscles are more similar to the latter pattern in maximizing twitch tension at the lower end of the temperature range, although they are broadly temperature independent (able to generate over 80% of maximal  $P_1$ ). At temperatures in excess of 40 °C, all muscles showed a decrease in  $P_1$  that is consistent with irreversible heat damage seen in other muscles (Ushakov 1963; Licht 1964). The twitch tension of the muscles of the tropical *Cnemidophorus* decrease sharply below 20 °C. This cold sensitivity in muscle tissue of a tropical organism is of interest and is worth further study.

Tetanic tensions are also thermally independent over a broad range in lizard muscles. At low temperatures (below 20 to 25 °C), tetanic tension decreases

with temperature in lizard muscles (Figs. 4 and 5) and the muscles of other organisms (Hill 1951; Hajdu 1951; Close and Hoh 1968; Fowler and Crowe 1976; Josephson 1981). High temperatures (above 40 °C) lead to a loss of tetanic tension in lizard muscle. The molecular basis for the thermal dependence of tetanic tension is not known.

The ratio of twitch/tetanic tension indicates the relative effect of temperature on these two parameters. Lizard muscles (Fig. 6), mammalian muscles (Close and Hoh 1968; Ranatunga 1977) and amphibian muscles (Hill 1951) show an increase in  $P_1/P_0$  with decreasing temperature. This may be the result of a longer period of activation during a twitch at cold temperatures (reflected by longer CT and 1/2 RT -

**Table 2.** Temperature coefficients for the isometric parameters of the IF and gastrocnemius muscles from 4 species of lizards

| Temperatures (°C)    | 10–15 | 15–20 | 20–25 | 25–30 | 30–35 | 35–40 | 40–45            | 45–47.5 |
|----------------------|-------|-------|-------|-------|-------|-------|------------------|---------|
| <i>Iliofibularis</i> |       |       |       |       |       |       |                  |         |
| <i>Dipsosaurus</i>   |       |       |       |       |       |       |                  |         |
| $P_t$                | 2.6   | 1.2   | 0.9   | 0.9   | 0.9   | 1.1   | 0.8              | 0.1     |
| $P_0$                | 3.1   | 2.1   | 1.7   | 1.2   | 1.0   | 0.9   | 0.5              | 0.0     |
| CT                   | 3.2   | 2.7   | 2.3   | 2.3   | 2.2   | 1.8   | 1.2              | 2.1     |
| 1/2 RT               | 4.1   | 3.1   | 3.0   | 2.0   | 2.2   | 1.7   | 1.7              | 3.2     |
| $dP_0/dt$            | 6.9   | 3.1   | 2.5   | 1.9   | 1.9   | 1.1   | 1.0              | 0.3     |
| <i>Cnemidophorus</i> |       |       |       |       |       |       |                  |         |
| $P_t$                | –     | 2.7   | 1.1   | 1.1   | 1.1   | 1.2   | 0.2              | –       |
| $P_0$                | –     | 4.0   | 1.9   | 1.1   | 1.0   | 0.8   | 0.1              | –       |
| CT                   | –     | 2.6   | 2.4   | 2.1   | 2.0   | 1.6   | 1.6              | –       |
| 1/2 RT               | –     | 5.7   | 3.8   | 2.4   | 1.9   | 1.9   | 1.0              | –       |
| $dP_0/dt$            | –     | 5.9   | 3.1   | 2.1   | 1.9   | 1.6   | 0.1              | –       |
| <i>Sceloporus</i>    |       |       |       |       |       |       |                  |         |
| $P_t$                | 1.5   | 1.1   | 1.1   | 1.0   | 1.2   | 0.6   | 0.2 <sup>a</sup> | –       |
| $P_0$                | 1.6   | 2.1   | 1.3   | 0.9   | 1.1   | 0.4   | 0.2 <sup>a</sup> | –       |
| CT                   | 3.2   | 2.5   | 2.1   | 1.8   | 1.9   | 1.9   | –                | –       |
| 1/2 RT               | 3.7   | 2.5   | 1.6   | 2.5   | 1.4   | 1.6   | –                | –       |
| $dP_0/dt$            | 2.4   | 2.4   | 1.8   | 1.8   | 2.2   | 0.4   | –                | –       |
| <i>Gerrhonotus</i>   |       |       |       |       |       |       |                  |         |
| $P_t$                | 1.1   | 0.9   | 0.9   | 1.1   | 1.1   | 0.4   | 0.0 <sup>a</sup> | –       |
| $P_0$                | 1.9   | 1.7   | 1.1   | 1.0   | 0.8   | 0.2   | 0.0 <sup>a</sup> | –       |
| CT                   | 3.2   | 2.4   | 2.0   | 1.7   | 2.5   | 1.4   | –                | –       |
| 1/2 RT               | 3.1   | 2.9   | 1.9   | 1.6   | 2.2   | 1.1   | –                | –       |
| $dP_0/dt$            | 2.1   | 1.4   | 1.6   | 1.7   | 2.2   | 0.3   | –                | –       |
| <i>Gastrocnemius</i> |       |       |       |       |       |       |                  |         |
| <i>Dipsosaurus</i>   |       |       |       |       |       |       |                  |         |
| $P_t$                | 1.3   | 0.8   | 0.8   | 0.8   | 0.8   | 1.4   | 0.9              | 0.4     |
| $P_0$                | 2.1   | 1.6   | 1.3   | 1.0   | 1.1   | 0.9   | 0.6              | 0.1     |
| CT                   | 3.4   | 3.3   | 2.5   | 2.4   | 2.1   | 1.7   | 1.7              | 1.3     |
| 1/2 RT               | 4.3   | 3.6   | 2.9   | 2.2   | 2.2   | 1.5   | 1.6              | 2.2     |
| $dP_0/dt$            | 4.5   | 2.8   | 2.3   | 1.9   | 1.6   | 1.6   | 1.2              | 0.2     |
| <i>Cnemidophorus</i> |       |       |       |       |       |       |                  |         |
| $P_t$                | 2.7   | 2.4   | 1.1   | 0.7   | 1.4   | 1.3   | 0.2              | –       |
| $P_0$                | 2.2   | 4.4   | 1.6   | 1.0   | 1.3   | 0.9   | 0.1              | –       |
| CT                   | 2.6   | 2.7   | 2.5   | 2.6   | 2.0   | 1.6   | 1.7              | –       |
| 1/2 RT               | 5.6   | 5.7   | 3.5   | 2.4   | 2.8   | 2.3   | 1.6              | –       |
| $dP_0/dt$            | –     | 6.4   | 2.0   | 1.5   | 2.3   | 1.8   | 0.1              | –       |
| <i>Sceloporus</i>    |       |       |       |       |       |       |                  |         |
| $P_t$                | 1.1   | 0.9   | 0.8   | 0.9   | 1.1   | 0.6   | 0.0              | –       |
| $P_0$                | 1.9   | 1.6   | 1.3   | 1.0   | 0.9   | 0.3   | 0.0              | –       |
| CT                   | 3.1   | 2.9   | 2.2   | 1.9   | 1.7   | 1.8   | 1.8              | –       |
| 1/2 RT               | 4.8   | 2.9   | 2.4   | 1.9   | 1.9   | 1.3   | 2.0              | –       |
| $dP_0/dt$            | 2.5   | 2.3   | 1.7   | 1.6   | 1.6   | 0.6   | –                | –       |
| <i>Gerrhonotus</i>   |       |       |       |       |       |       |                  |         |
| $P_t$                | 1.1   | 1.0   | 0.9   | 1.0   | 1.2   | 0.3   | 0.0 <sup>a</sup> | –       |
| $P_0$                | 2.3   | 1.9   | 1.2   | 1.0   | 1.0   | 0.1   | 0.0 <sup>a</sup> | –       |
| CT                   | 3.0   | 2.4   | 2.2   | 2.1   | 1.7   | 1.6   | –                | –       |
| 1/2 RT               | 3.1   | 1.7   | 3.2   | 1.4   | 1.2   | 1.4   | –                | –       |
| $dP_0/dt$            | 3.0   | 2.0   | 1.8   | 1.6   | 2.3   | 0.2   | –                | –       |

<sup>a</sup> For the temperature range 40–42.5 °C

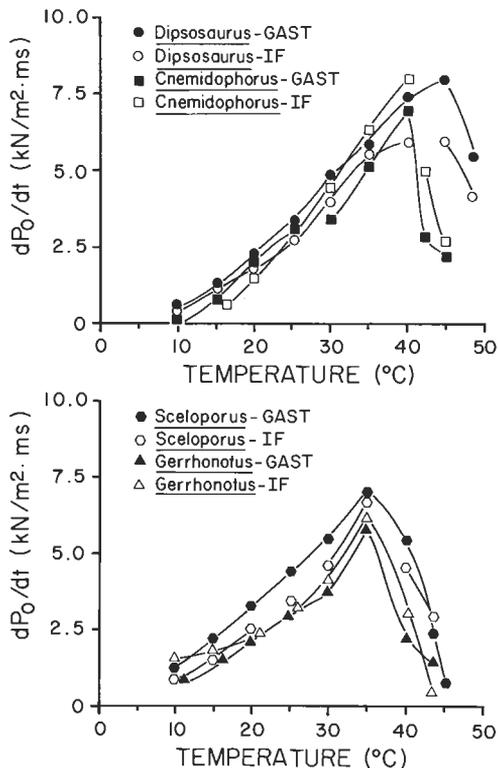


Fig. 8. The maximal rate of tension rise during a tetanus ( $dP_0/dt$ ) as a function of temperature in the IF (open symbols) and gastrocnemius (closed symbols) muscles of 4 lizard species. Points represent the mean  $dP_0/dt$  for all muscles from a given species at that temperature. Lines connecting two points indicate they are significantly different at the 0.05 level of significance using a paired  $t$ -test (Dixon and Massey 1969)

see below) which more than compensates for the decrease in  $V_{\max}$  at low temperatures. In addition, this increase in  $P_i/P_0$  probably reflects more complete activation of the muscle in response to a single twitch at lower temperatures (Ranatunga 1977). At  $10^\circ\text{C}$ , with a  $P_i/P_0$  of nearly 0.8, the differences between muscle response to twitch versus tetanic stimulation are small. The increase in  $P_i/P_0$  with temperatures above  $40^\circ\text{C}$  is presumably due to a decrease in  $P_0$  at high temperatures. At these temperatures,  $P_i$  is probably less affected than  $P_0$  due to the increase in  $V_{\max}$  (reflected by the continual increase in CT with increasing temperature above  $40^\circ\text{C}$ ). Clearly, twitch and tetanic tensions do not have similar thermal dependencies.

The twitch time course (as measured by CT and  $1/2$  RT) decreased with increasing temperature up to the highest temperatures tested in lizard muscles. This pattern is commonly observed in the muscles of a variety of organisms (Close and Hoh 1968; Josephson 1981; Petrofsky and Lind 1981). This increment is presumably the result of both an increased rate of  $\text{Ca}^{++}$  release and a greater activity of actomyosin

ATPase (reflected in CT) and an increased rate of removal of  $\text{Ca}^{++}$  by pumps located on the membranes of the sarcoplasmic reticulum (reflected in  $1/2$  RT). While the muscles of these lizard species all show a similar response of twitch duration to temperature, any absolute twitch duration (CT +  $1/2$  RT) in the muscles of *Sceloporus* and *Gerrhonotus* occurs at a temperature  $10^\circ\text{C}$  less than in the muscles of *Cnemidophorus* and *Dipsosaurus*. This differential may in part be due to the smaller size of *Sceloporus* and *Gerrhonotus*, since smaller animals should in general have faster muscle (Hill 1950).

The maximal rate of tension rise ( $dP_0/dt$ ) should increase with increasing temperature due to 2 factors: 1) a temperature mediated increase in maximal tetanic tension; and 2) a temperature mediated increase in the maximal velocity of shortening of the muscle. Therefore,  $dP_0/dt$  should reflect the thermal dependencies of both tension and kinetic parameters. The  $dP_0/dt$  is strongly temperature dependent and shows a clear maximum at  $40$ – $45^\circ\text{C}$  in *Dipsosaurus*,  $40$ – $42.5^\circ\text{C}$  in *Cnemidophorus* and  $35^\circ\text{C}$  in *Sceloporus* and *Gerrhonotus*. Therefore, in 3 of 4 species, there is a good correlation between  $dP_0/dt$  and PBT (see below). Maximal rate of tension rise is the isometric parameter which best correlates with the isotonic maximal velocity of shortening ( $V_{\max}$ ) in rat muscle (Close 1964). Because of the relative ease of measuring  $dP_0/dt$ , it would be useful to verify this correlation in a variety of systems so that  $dP_0/dt$  might be used as an index of  $V_{\max}$ . In this regard,  $dP_0/dt$  does have a similar thermal dependence to  $V_{\max}$  in *Dipsosaurus* IF muscle (Marsh and Bennett 1981).

Many studies have attempted to correlate the thermal dependencies of various physiological parameters with the behaviorally selected PBT of lizard species (for a review see Dawson 1975). Among the parameters that have been shown to be maximized at PBT are heart rate increment (Licht 1965), maximal sustainable walking speed (Moberly 1968 a, b), and maximal energy mobilization during burst activity (Bennett and Dawson 1972). Of the measured isometric muscle parameters, only  $dP_0/dt$  and upper thermal tolerance show a good correlation with the PBT of these species. It appears that these lizard species maximize both tension generation and contractile speed at high body temperature, although neither one alone is maximized at PBT. The exception to the correlation between PBT and maximal  $dP_0/dt$  is *Gerrhonotus*, which would apparently benefit in muscle performance by maintaining a higher body temperature than it does under field conditions. *Gerrhonotus* has a low burst running speed and is more reclusive and relies more heavily on static defense mechanisms than do the other 3 species of lizards examined here (Ben-

nett 1980). These differences may obviate the need for the maintenance of a high body temperature to maximize muscle performance and other benefits to the maintenance of a lower body temperature, such as reduced energy costs, reduced exposure to predation and the availability of low temperature habitats can be realized.

In addition to the correlation of  $dP_0/dt$  with PBT, the isometric properties of lizard muscles show other adaptations to their thermal environment. The twitch kinetic parameters show a clear change with the rate-temperature curves for CT and 1/2 RT located to the left in the less thermophilic species, *Gerrhonotus* and *Sceloporus*. A twitch is as fast at 30 °C in a *Gerrhonotus* or *Sceloporus* muscle as a muscle twitch at 40 °C in *Dipsosaurus* or *Cnemidophorus*. The other thermal adaptation obvious in the muscle tissues is the shift in the high temperature thermostability in the muscles of these species in concert with their upper critical thermal maxima.

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