BODY SIZE, MUSCLE POWER OUTPUT AND LIMITATIONS ON BURST LOCOMOTOR PERFORMANCE IN THE LIZARD *DIPSOSAURUS DORSALIS*

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Summary

The power output of fast-glycolytic (FG) muscle fibres isolated from the iliofibularis (IF) muscle of desert iguanas (*Dipsosaurus dorsalis*) was measured at 35°C using the oscillatory work-loop technique. To simulate cyclical muscle length changes during running, isolated fibre bundles were subjected to sinusoidal length changes and phasic stimulation during the strain cycle. At constant strain (12%), the duration and timing (phase) of stimulation were adjusted to maximise power output. Using both hatchlings (4–8g) and adults of varying sizes (15–70g), the intraspecific allometries of IF length and contractile properties were described by regression analysis. The muscle length at which isometric force was maximum (L_0, mm) increased geometrically with body mass (M, g) ($L_0 = 5.7 M^{0.33}$). Maximum power output and the force produced during shortening showed no significant relationship to body size; work output per cycle (W_{opt}, Jkg^{-1}) under conditions required to maximise power did increase with body size ($W_{opt} = 3.7 M^{0.24}$). Twitch duration (T_d, ms), measured from the onset of force generation to 50% relaxation, increased allometrically with body mass ($T_d = 12.4 M^{0.18}$). Limb cycling frequency during burst running (f, reported in the literature) and the frequency required to maximise power output *in vitro* (f_{opt}) decreased with body size, both being proportional to body mass raised to the power 0.24. These findings suggest that limb cycling frequency may be limited by twitch contraction kinetics. However, despite corresponding proportionality to body size, limb cycling frequencies during burst running are about 20% lower than the cycling frequencies required to maximise power output. Differences in the contractile performance of the IF *in vitro* and *in vivo* are discussed in relation to constraints imposed by gravitational forces and the design of muscular, nervous and skeletal systems.

Introduction

Hill (1950) developed a simple model for the scaling of running parameters in 'geometrically similar' animals, i.e. in animals in which the length of anatomical elements, *l*, is proportional to mass$(M)^{1/3}$ and diameter$(d)^{1.0}$ (see also McMahon, 1984). This model predicts that animals of different size should be able to run at the same linear

speed and jump the same height. A few studies are in agreement with the theoretical expectations of this model. For example, maximal running speed and interspecific differences in body size are independent within three orders of mammals (Artiodactyla, Carnivora and Rodentia) and within three families of lizards (Iguanidae, Scinidae, Teiidae) (Garland 1982, 1983). However, in most studies maximal running speed is mass-dependent, larger animals being able to run faster than smaller animals (reviewed in Schmidt-Nielsen, 1984). The maximum burst speeds of a number of lizard species have been shown to increase with body size (positive allometry) within a single species (Huey, 1982; Garland, 1982; Huey and Hertz, 1982; Hertz *et al.* 1983; Losos *et al*. 1989; Snell *et al.* 1988) and amongst species of a single genus (Losos, 1990). For example, the maximum burst speed of the agamid, *Stellio stellio* is proportional to the body mass to the 1/3 power (Huey and Hertz, 1982). In contrast, in two species of iguana, *Ctenosaura similis* (Garland, 1985) and *Dipsosaurus dorsalis* (Marsh, 1988), maximum sprint speed is relatively independent of size from hatchlings to fully grown adults.

McMahon (1974, 1975) proposed that animals do not scale geometrically but rather maintain 'static stress similarity' ($l \propto d^{1/2}$ or $M^{1/5}$ and speed $\propto M^{2/5}$) or 'elastic similarity' ($l \propto d^{2/3}$ or $M^{1/4}$ and speed $\propto M^{1/5}$), whereby animals of increasing size thicken their proportions, preventing 'buckling' under lateral displacement of the body. The speed at the trot–gallop transition point, believed to be a 'physiologically equivalent' speed for different-sized animals, has been reported to scale according to elastic similarity in mammals (Heglund *et al.* 1974; Pennycuick, 1975). In contrast, in a review of data for maximal running speeds (MRS) in terrestrial mammals, Garland (1983) found that MRS scales as $M^{0.17}$. This exponent is in agreement with Gunther's (1975) model of 'dynamic similarity', whereby homologous parts of different-sized animals experience similar net forces.

Few studies have attempted to determine adjustments in muscle contractile properties that may accompany size-dependent changes in locomotor behaviour. The maximum shortening velocity (V_{max}) of fast-glycolytic (FG) fibres (recruited for burst speed running) is nearly independent of body size ($V_{max} \propto M^{0.07}$) among mammals (Rome *et al*. 1990). V_{max} and the velocity of shortening required for maximum power output are essentially independent of body size in fast muscle fibres isolated from dogfish (*Scyliorhinus canicula*; Curtin and Woledge, 1988), salamanders (*Ambystoma tigrinum*; Bennett *et al.* 1989) and desert iguanas (*Dipsosaurus dorsalis*; Marsh, 1988). Interestingly, a positive allometric relationship between twitch duration and body size has been demonstrated in fish (Wardle, 1975; Archer *et al.* 1990; Altringham and Johnston, 1990), lizards (Marsh, 1988) and amphibians (Bennett *et al.* 1989). Altringham and Johnston (1990) found that the cycle frequency required to maximise power output from fast-twitch fibres during repetitive contractions decreased with body size in cod (*Gadus morhua*). These changes were correlated with an increase in twitch duration and with developmental changes in the pattern of innervation of these muscle fibres (Altringham and Johnston, 1990; Archer *et al.* 1990). An increase in twitch duration is probably due largely to a decrease in the rate of muscle deactivation; the initial activation processes are sufficiently rapid that they govern only a small part of the total twitch duration (Josephson, 1975; Cannell, 1986; Marsh, 1990). Increased rates of deactivation are

achieved through factors influencing the time course of Ca^{2+} regulation (Ready, 1986). For example, in fast muscle fibres of the insect *Neoconocephalus robustus* an increase in twitch duration during development is correlated with an increase in the ratio of myofibril volume to that of sarcoplasmic reticulum and T-tubules (Josephson and Young, 1987).

This study examines the match between the allometry of running speed and muscle contractile kinetics in the desert iguana *Dipsosaurus dorsalis*. Burst locomotion in this lizard is powered by fast muscle fibres (Jayne *et al.* 1990). The iliofibularis muscle is important in femoral retraction and crural flexion of the hindlimb during locomotor activity (Snyder, 1954; Jayne *et al*. 1990). It contains approximately 70% fast glycolytic fibres (FG) in this species (Gleeson *et al.* 1980). Size-dependent changes in the twitch contraction kinetics of these muscle fibres are associated with changes in burst limb cycling frequency (Marsh, 1988). In a companion study (Swoap *et al.* 1993), we found that there is a correlation between twitch duration at low body temperatures and the cycle frequency required to maximise power output during oscillatory work. The goal of the following study was to determine whether the changes in twitch contraction kinetics with body size are reflected in changes in the operating frequency of the muscle at which mechanical power output is maximal.

Materials and methods

Animals

Desert iguanas, *Dipsosaurus dorsalis* Hallowell, were captured near Palm Springs, California, in June–August 1991. Adults and juvenile animals weighed 15–70g and hatchlings 4–5g. Animals were maintained under natural light regimes (8h dark; 16h light) in glass aquaria with a heat source and shelter to permit behavioural thermoregulation. Food consisted of green leafy material and protein supplements supplied *ad libitum*. The sides of the aquaria were sprayed twice a week with water to prevent dehydration. Animals were maintained for up to 21 days prior to experimentation. No significant differences were observed in the results from fresh specimens and those maintained for up to 3 weeks.

Muscle fibre preparation

Animals were anaesthetized using halothane vapour, weighed and subsequently killed by decapitation. The skin from the pelvic region and hindlimbs was removed and the body immersed in Ringer's solution containing $145 \, mmol \, l^{-1}$ NaCl, $4 \, mmol \, l^{-1}$ KCl, $20 \, mmol \, l^{-1}$ $NaHCO_3$, $1 \, mmol \, l^{-1}$ $MgCl_2$, $2.5 \, mmol \, l^{-1}$ $CaCl_2$ and $11 \, mmol \, l^{-1}$ glucose, pH7.5 at 35˚C (modified from Marsh and Bennett, 1985). The iliofibularis (IF) muscle was removed along with the distal tendon and a portion of the connected pelvis (see Swoap *et al*. 1993 for details). Both limbs were dissected to provide two preparations in case the first failed; only one preparation from each animal was used in the analyses. The red region of the IF containing slower muscle fibre types was removed and discarded to leave only fast-twitch, glycolytic fibres (FG). Surgical silk was used to attach the section of pelvis to the transducer and the distal tendon to a hook and small gold chain for

attachment to the ergometer used for length control. The pH of the Ringer in the chamber was maintained at 7.4–7.6 by bubbling with 95% O_2:5% CO_2.

Apparatus

The muscle was mounted in a small Perspex chamber containing 20ml of Ringer. The temperature of the Ringer was controlled ($\pm$0.1°C) using a heating element and cooling coil incorporated into the chamber. The muscle bundles were suspended between a force transducer below and an ergometer servo control unit above. Force was measured using a transducer consisting of Entran strain gauges (ESU-060-100) attached to either side of a stainless-steel bar (sensitivity $10\,g\,V^{-1}$). Muscle length was controlled using an ergometer (Cambridge Technology 300H, Cambridge, MA, USA) mounted on an adjustable arm. The frequency and magnitude of imposed length fluctuations (strain) and the timing of stimulation in relation to the strain cycle (phase) were controlled with custom-designed hardware. Preparations were stimulated using platinum electrodes lying either side of the fibre bundles connected to a Grass S48 stimulator and current amplifier (in-house design). The control and output signals from the apparatus were collected and stored with a Metrabyte A/D board installed in an IBM-PC computer with in-house software.

Experimental protocol

All contractile measurements were made at 35°C, a temperature at which preparations are viable for many hours and produce close to maximum power output (see Swoap *et al*. 1993). Muscle fibre length (recorded to within 0.5mm) and stimulus strength and duration (typically 1ms and 20V) were adjusted to produce maximal twitch tension. The time from the onset of force to peak tension (time to peak tension, T_{PT}), the time from the peak to 50% relaxation ($R_{T1/2}$), and the time from the onset of force to 50% relaxation (twitch duration, T_d) were measured for the twitch. For measurements of oscillatory work, muscles were subjected to sinusoidal length changes and stimulated at a selected point (phase) in the strain cycle. The force and length records were then plotted to produce a 'loop', the area of which represented the work done in a single strain cycle (Josephson, 1985). Muscles were subjected to four cycles in each experimental run. Work per cycle stabilized by the third cycle, which was used for analyses. Trains of stimuli (1ms duration) were given at a frequency required to produce a maximum fused tetanus (typically 200–250Hz for adults, 300–350Hz for hatchlings). Power output was maximised at a range of cycle frequencies by varying the duration and timing (phase) of stimulation (see Johnson and Johnston, 1991). Experimental runs were performed at 10min intervals. Reproducible results were obtainable for many hours.

Statistics

Intraspecific allometries were determined from log-transformed values of the cycle frequency required to maximise power output (defined as the optimal cycle frequency, f_{opt}), power output, work done per cycle, twitch contraction kinetics and muscle length. Regression lines were determined with the program SPSS (SPSS Inc., Michigan) from

standard least-squares regression [log(variable) on log(mass)] and F-statistics used to determine the significance of any underlying relationship (Sokal and Rohlf, 1981). In addition, reduced major axis (RMA) analysis was used to measure relationships between physiological variables and body size. RMA is considered by some to be a less biased approach for estimating slopes (Rayner, 1985; but see Marsh, 1988).

Results

The results of the allometric analyses are summarised in Table 1. Twitch rise time (T_{PT}) and duration T_d increase allometrically with body size ($P<0.001$; Table 1; Fig. 1). Although the correlation between $\log R_{T1/2}$ and $\log M$ is not significant (Table 1; $r=0.412$, $P=0.058$; see also Marsh, 1988), a highly significant correlation existed between $R_{T1/2}$ and body size before log-transformation ($r=0.655$, $P<0.001$). The length of the IF muscle at which isometric force is maximal (L_0) increases with body size approximately in accordance with the model of geometric similarity (Hill, 1950), i.e. it increases in proportion to the body mass raised to the power 1/3 (Table 1). The results for regression analyses of twitch contraction kinetics (reduced major axis and standard least squares) are in close agreement with previous investigations on the same muscle in *Dipsosaurus* (Marsh and Bennett, 1985; Marsh, 1988).

Stride length (L_s) and hindlimb length (L_{HL}) are naturally related (Sukhanov, 1968; Garland, 1985; Losos, 1990). Both L_s and L_{HL} for *Dipsosaurus* scale similarly ($L_s \propto M^{0.271}$ and $L_{HL} \propto M^{0.289}$; Table 1 of Marsh, 1988). This similarity in scaling suggests that limb movements are similar in small and large animals and, therefore, so are the strain fluctuations of the IF during burst running. Preliminary observations showed that a strain of 12% (6% above and below resting length) produced maximum power output in muscles from hatchlings and adults over a wide range of cycle frequencies (see also Swoap *et al*. 1993). Therefore a strain of 12% was used in all work-loop measurements.

The power–frequency curves of the IF muscles have a well-defined maximum (Fig. 2). As body size increases, the cycle frequency at which power output is maximum decreases from around 23 Hz in hatchlings (4–8 g) to 10 Hz in fully grown adults (60–70 g; $f_{opt}=34.9M_b^{-0.237}$, $P<0.001$; Figs 2 and 3). The proportional decrease in the optimal cycle frequency for power output with increasing animal size is almost identical to the decrease in limb cycling frequency (f) with increase in animal size ($f=26.2M^{-0.238}$; Marsh, 1988), although absolute values differ (Fig. 3). Work per cycle for a given volume of muscle increases with body size (Fig. 4). Maximum mass-specific power output and the force measured at L_0 during the shortening phase of the strain cycle, however, are independent of animal size (Figs 5 and 6). The average maximum power output was $135\pm6.9\,\mathrm{W\,kg^{-1}}$ (s.e., $N=21$; 95% confidence limits 120–149 $\mathrm{W\,kg^{-1}}$). In Fig. 7, the possible effects of changes in the isometric properties on the work output of the muscle are shown, although it must be remembered that shortening-induced deactivation and stretch activation during muscle sinusoids will increase the capacity of the muscle to generate force during shortening (Josephson and Stokes, 1989).

Table 1. *The results of regression analyses (least mean squares and reduced major axis) showing ontogenetic allometries for contractile variables measured from fast-twitch fibres of the IF from* Dipsosaurus dorsalis *at 35 °C*

	Regression (log$y$ on log$M$)				Reduced major axis		
y	r	a	b	95% confidence interval	a	b	95% confidence interval
Work loops							
Optimal frequency (Hz)	0.893	34.9	−0.237	−0.181 to −0.293	38.0	−0.266	−0.209 to −0.338
Maximum power (W kg^{-1})	0.120	NS					
Optimal work (J kg^{-1})	0.699	3.7	0.238	0.121 to 0.354	2.8	0.325	0.193 to 0.546
Tension (kN m^{-2})	0.348	NS					
Twitch kinetics							
T_{PT} (ms)	0.735	6.9	0.212	0.121 to 0.305	5.4	0.290	0.183 to 0.460
$R_{T1/2}$ (ms)	0.412	NS					
T_d (ms)	0.722	12.4	0.184	0.102 to 0.266	10.0	0.255	0.158 to 0.343
Muscle length							
L_O (mm)	0.947	5.7	0.330	0.278 to 0.382	5.4	0.349	0.298 to 0.409

Following log transformation, data were analysed using standard least-squares regression (log$y$ on log$M$) and reduced major axis regression. Data are described by the equation: log$y$=a+$b$log$M$. Optimal frequency, the frequency at which power output was maximal; Maximum power, maximum power output; Optimal work, the work output per cycle under conditions where power output was maximal; tension, tension developed at L_0 during shortening in a single strain cycle under optimal conditions for work output; T_{PT}, time from onset of twitch to peak force; $R_{T1/2}$, time from peak force to 50% relaxation; T_d, twitch duration represented as the time from the onset of force generation to 50% relaxation; NS, not significant.

Discussion

Allometry of V*max* *and twitch contraction kinetics*

Hill (1950) predicted that the maximum shortening velocity of a muscle (V_{max}) and its shortening velocity during locomotory activity (V) should decrease in the same proportion as body size increases. Rome *et al*. (1988) examined the importance of the ratio of V/V_{max} in slow muscle fibres of carp (*Cyprinus carpio*). They proposed that
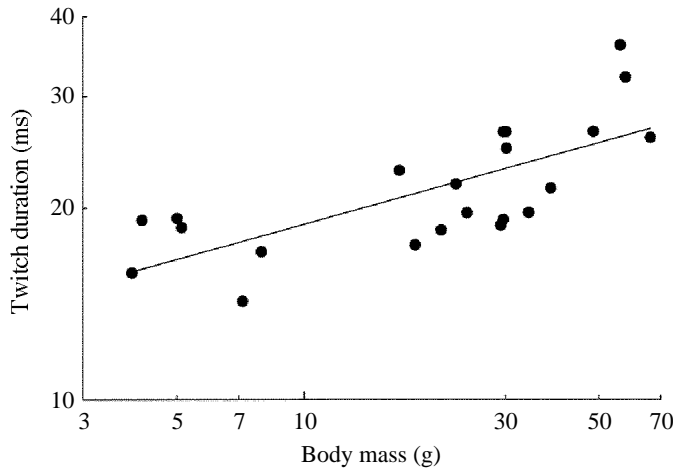

Fig. 1. The relationship between twitch duration (T_d, onset to 50% relaxation) and body size in *Dipsosaurus dorsalis*. The solid line is the least-squares regression line (equation in Table 1).
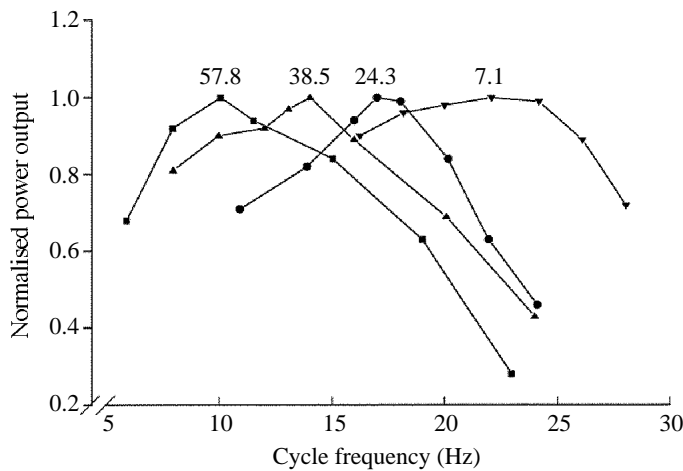
Fig. 2. Power–frequency curves for representative iliofibularis preparations performing oscillatory work (35°C). The mass of the animal (in grams) from which the preparation was obtained is indicated above each curve. The maximum power output for a range of frequencies was determined by systematic adjustment of the stimulus timing and duration at a strain of 12%. Data are normalised to the maximum power output obtained for each preparation.

muscles work over a limited range of V/V_{max} values, in this way generating near-maximal power at high efficiency. The ratio V/V_{max} is thought to represent a 'design constraint' for fish during steady swimming (Rome *et al.* 1988, 1990). In mammals, stride frequency and V_{max} in slow soleus muscles both decline with increasing animal size in a manner which would tend to keep V/V_{max} constant (Rome *et al.* 1990). However, V_{max} is relatively
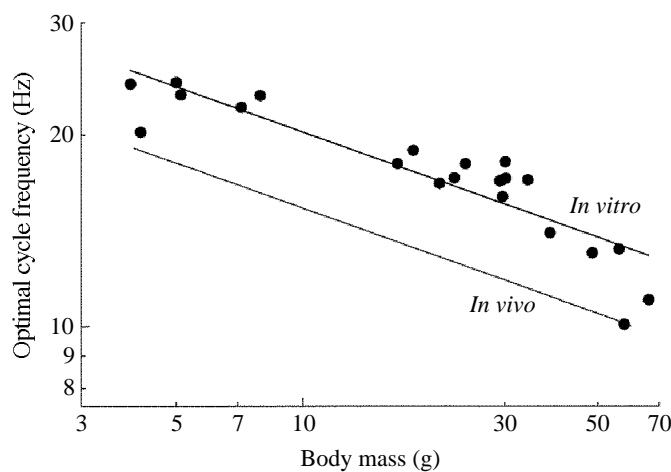
Fig. 3. The relationship between the cycle frequency at which power output was maximal (optimal cycle frequency) and body mass (35°C). The upper line represents the least-squares regression line (equation given in Table 1). The lower line is the relationship between limb cycling frequency during burst running and body size (from Marsh, 1988).
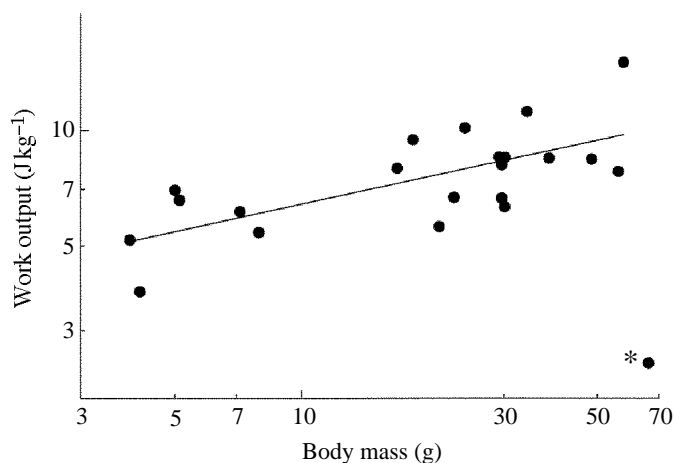
Fig. 4. Work done per cycle (mass-specific, Jkg^{-1} freshmass) normalised to preparation mass under conditions that maximised power output as a function of body mass (35°C). The solid line represents the least-squares regression line (equation in Table 1). One preparation, marked by an asterisk in this and two following figures, had an unusually low value for work output, possibly because of fibre damage. This value was not used in deriving the regression line.

independent of body size in fast-twitch fibres of mammals (Rome *et al.* 1990) and of dogfish (Curtin and Woledge, 1988). In *Dipsosaurus dorsalis*, V_{max} (Marsh, 1988) and shortening velocity *in vivo* (see below) are relatively independent of body size in FG fibres, consistent with the constancy of V/V_{max} for maximum power output.

In contrast to the independence of V_{max} on body size, twitch contraction kinetics do change as animals grow. Developmental changes in twitch contraction kinetics have been correlated with the frequency of locomotor movements during burst activity for fish (Wardle, 1975), amphibians (Bennett *et al.* 1989) and reptiles (Marsh, 1990), including
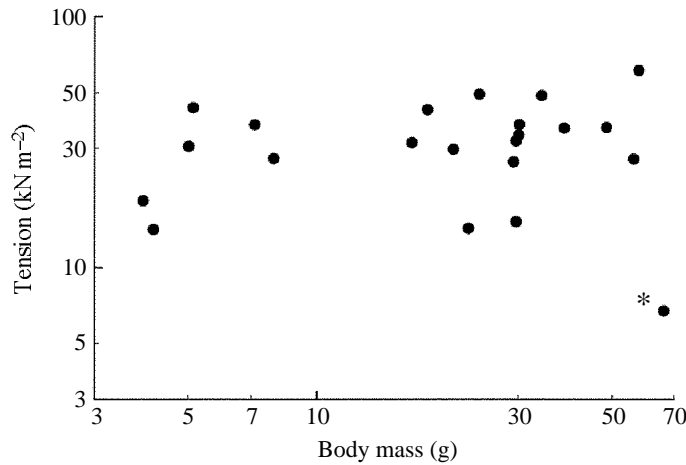

Fig. 5. The tension ($kN\,m^{-2}$) developed during oscillatory work at L_0, under conditions that maximised power output, as a function of body mass (35°C). Values are normalised for cross-sectional area (preparation mass divided by length, assuming a density of $1\,g\,ml^{-1}$ for muscle).
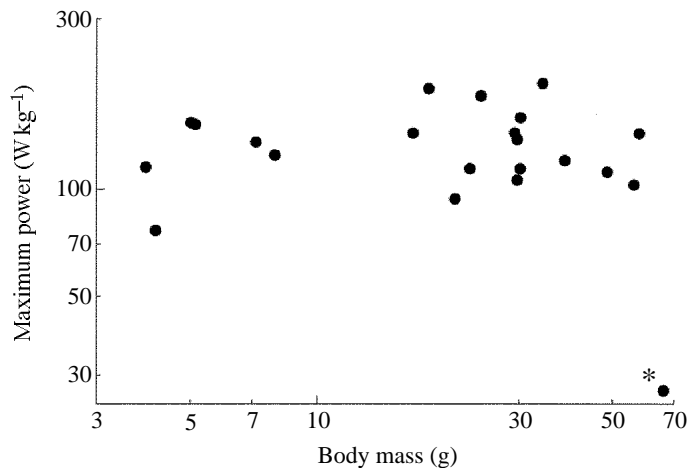

Fig. 6. Maximum power output (mass-specific, $W\,kg^{-1}$ freshmass) as a function of body mass (35°C).

A

Hatchling Adult

20 mN

20 ms

Hatchling Adult

22 Hz 16 Hz

B

Hatchling Adult
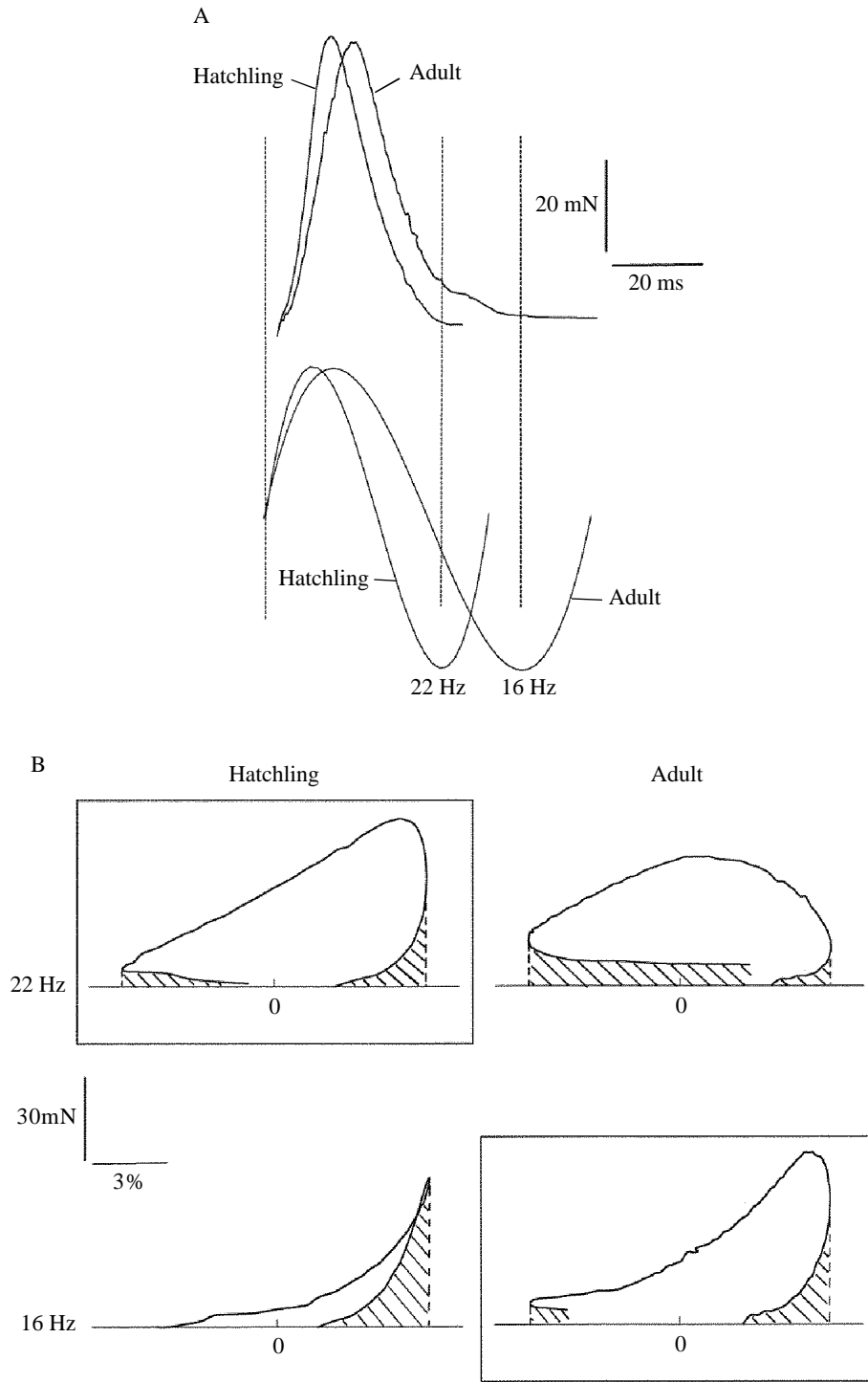
22 Hz 0 0

30mN

3%

16 Hz 0 0

Fig. 7

Fig. 7. (A) Isometric twitches at 35°C for preparations isolated from an adult (30g) and a hatchling (7g) lizard. The cycle frequencies of strain fluctuations that maximised power output in adult (16Hz) and hatchling (22Hz) preparations are also shown. The two dashed lines to the right of the force records are drawn to show the onset of the stretch half of the cycle; force produced during the stretch represents negative work. (B) Hypothetical work loops generated by plotting twitch force against strain (expressed as a percentage of resting length) at 22Hz and 16Hz. The timing of force production (phase) is that which maximised power output at 22Hz for hatchlings and 16Hz for adults (determined experimentally). The area inside the loop is the net positive work done by the muscle; the hatched area represents negative work. Work loops in the boxes are those in which theoretical work output is maximal. Note, at high frequencies, the adult muscle fibres fail to relax following shortening, force being generated during lengthening (negative work). At low frequencies, positive work output is compromised in hatchling fibres since the time course of force production during shortening (positive work) is reduced.

Dipsosaurus (Marsh, 1988). These changes in twitch duration have also been associated with changes in the optimal cycle frequency for power output in cod *Gadus morhua* (Altringham and Johnston, 1990) and now in *Dipsosaurus dorsalis* (Figs 1 and 2). In *Dipsosaurus*, the duration of the isometric twitch (T_d) occupies 0.746 ± 0.061 of half the strain cycle at f_{opt} in individuals of all sizes (mean$\pm$S.D., 95% confidence interval 0.693–0.800, $N=22$). Both optimal cycle frequency and stride frequency change in a similar way with body size (Fig. 3). Thus, as an animal grows, there is an increase in twitch duration (Fig. 1) and an associated increase in stride duration (decrease in stride frequency; Fig. 3), tending to keep the ratio of twitch duration to cycle duration constant, at least at a single temperature. Because of different temperature coefficients for twitch duration and burst limb cycling frequency, the actual ratio of the two is a function of temperature (see Swoap *et al.* 1993 for further discussion). The studies mentioned above on fish muscle have emphasized the constancy of V/V_{max} as a 'design constraint'. From our study it appears that the ratio of twitch duration to cycle duration is a similar 'design constraint' for muscle operation *in vivo*.

Oscillatory work

To maximise net work output, force must be developed during, and confined to, the shortening half of the strain cycle. An increase in the duration of the twitch as the animal grows would increase the chance of force being produced during the lengthening portion of the strain cycle, creating negative work, if the muscles were to operate at the high cycling frequencies characteristic of small animals (Fig. 7A,B). Thus, twitch contraction kinetics set the upper limit of cycling frequencies over which net work remains positive.

Why power output declines at low cycle frequencies is not obvious. For animals of all size there is a bell-shaped relationship between operating frequency and power output (Fig. 2). The power output at the optimal cycle frequency is independent of animal size (Fig. 6). Thus, at a frequency which is sub-optimal for the muscle of a small animal, the specific power output is less than that for the muscle of a larger animal at the same frequency (Fig. 2). Surely an 'adult twitch' can be simulated by increasing the duration of stimulation given to hatchling muscle fibres, partially tetanising them and increasing the time course of force production during shortening and thereby increasing work output

(Fig. 7). Compared to adult muscle fibres, the faster rates of deactivation in hatchlings may be achieved by increasing the rate of Ca^{2+} pumping which incurs a significant cost (Marsh, 1990); fatigue may thus contribute to the observed decline in work/power output at low frequencies and the associated long stimulus durations in muscle fibres from hatchling lizards. The possible effects of parvalbumin on relaxation rate and therefore the capacity to do work during prolonged stimulation in this muscle is also the subject of further investigation.

The optimal cycling frequency for power output *in vitro* (f_{opt}) and limb cycling frequency *in vivo* (f; Marsh, 1988) change in exactly the same way with increasing animal sizes ($f_{opt} \propto M^{-0.237}$, $f \propto M^{-0.238}$; see Fig. 3). This correspondence presumably reflects the importance of muscle contractile performance in determining the characteristics of burst running behaviour. The optimal cycling frequency for power output (*in vitro*) is about 20% greater than the maximum stride frequency for animals of all size (Fig. 3). Interestingly, at lower temperatures, limb cycling frequency and the optimal cycling frequency for power output are more closely matched (Swoap *et al.* 1993). The reasons for the seemingly sub-optimal stride frequency are unclear. Constraints on *in vivo* operation may be imposed on the muscle by the elastic storage and inertial loading at high temperatures and associated high operating frequencies. Inertial loads are experienced particularly at high speeds and include forces imposed by the body mass during ground contact and the mass of the limb during the recovery stroke (Marsh, 1990). Thus, the limb cycling frequency adopted by the animal and ultimately the maximal running speed may represent a compromise between the increasing losses incurred through inertial loading as maximal velocity increases and the additional power available to accelerate the body with increasing operating frequency.

Implications for running performance

In accordance with the prediction of Hill's (1950) model of geometric similarity, burst running speed is independent of body size in *Dipsosaurus dorsalis* (Marsh, 1988). In this study we have attempted to assess the validity of the assumptions and predictions of Hill's model and to determine the importance of muscle contractile performance on the relationship between running speed and body size.

Burst limb cycling frequency and the optimal cycling frequency for power output change in the same way with body size. Thus, if we assume that animals of different size maximise work output per cycle at the cycling frequency chosen, work done per cycle and power output *in vivo* will also change in a similar manner with body size as measured *in vitro*. The model of 'geometric similarity' assumes that force/cross-sectional area is constant over body size (Hill, 1950). Marsh (1988) found that the maximum isometric force/cross-sectional area that the muscle was capable of producing and the shape of the force–velocity curve were independent of body size. Likewise, the force produced at resting length during sinusoidal shortening is independent of body size (Fig. 5). Thus, hatchling and adult animals are operating at a similar point on the force–velocity curve, producing similar forces (Fig. 5) at equivalent shortening velocities (see below). The model of geometric similarity also predicts that work/contraction for a given volume of muscle should be independent of body size and that the power expended during running

should be relatively larger in small animals (i.e. power available for running $\propto M^{2/3}$; Hill, 1950). Work per cycle increases with size, the increase being inversely proportional to the change in optimal cycle frequency (i.e. $W_{opt} \propto M^{0.238}$, $f_{opt} \propto M^{-0.237}$) (Table 1; Figs 3 and 4). Mass-specific power output is equal to the product of mass-specific work per cycle and the cycle frequency and is therefore independent of body size (Fig. 6):

$$\text{Power} = W_{opt} \times f_{opt}.$$

Therefore:

$$\text{Power} \propto M^{0.24} \times M^{-0.24} \propto M^0. \tag{1}$$

Assuming geometric similarity for hindlimb muscle mass for hatchling and adult individuals, the 'absolute power' available for burst running (W) will increase linearly with body mass ($M^{1.0}$) rather than being relatively larger in smaller animals.

Hill's (1950) model predicts that for gemetrically similar animals muscle shortening velocity (*V*) and running speed should be independent of body size. In *Dipsosaurus*, if the muscle shortens in time $\Delta t (\propto 1/f_{opt} \propto M^{-0.24})$ and muscle length (L_0) is proportional to $M^{0.33}$:

$$V = L_0/\Delta t.$$

Therefore:

$$V \propto M^{0.33} \times M^{-0.24} \propto M^{0.09}. \tag{2}$$

If one assumes geometric similarity, muscle length is proportional to limb length and thus shortening velocity (*V*) is also a measure of running speed (Hill, 1950).

However, hatchling and adult lizards are not necessarily geometrically similar and thus the relative proportions of limb and body size may change during growth. Relative changes in limb and body dimensions have previously been correlated with maximum sprint performance in lizards (Garland, 1985; Losos, 1990). For example, hindlimb length is positively correlated with sprint performance in *Anolis* lizards (Losos and Sinervo, 1989). Thus, if the hindlimb completes a single cycle in time $t (\propto 1/f)$ and the length of the hindlimb (L_{HL}) is proportional to $M^{0.29}$ (Marsh, 1988) then L_{HL}/t also represents a measure of burst running velocity (V_R):

$$V_R \propto L_{HL}/t.$$

Therefore:

$$V_R \propto M^{0.29} \times M^{-0.24} \propto M^{0.05}. \tag{3}$$

By comparing relationships 2 and 3, one can see how the proportionally longer hindlimbs in smaller individuals of *Dipsosaurus dorsalis* are thought to contribute to similar sprint running speeds observed in adults and hatchlings (Marsh, 1988). Relative muscle mass has also been shown to be important in determining the scaling of maximum running speeds: in the Australian lizard *Amphibolurus nuchalis* relative thigh muscle mass and maximum running speed increase with body size (Garland, 1985). Proportionally larger limb muscle mass in hatchlings of *Dipsosaurus* would clearly contribute to the observed independence of burst running speed on size.

The analyses presented here represent a modification of 'geometric similarity' based upon muscle contractile performance under conditions more relevant to locomotion (than

are isometric and isotonic contraction). The net result is roughly the same; maximal running speed is relatively mass-independent ($\propto M^{0.09}$) although the assumptions of the original model are clearly inaccurate. Whether these predictions represent general properties of limb muscle or simply those of *Dipsosaurus* remains to be tested. It would be useful in testing these predictions to determine whether the same relationships hold in species in which there is a positive allometry between body size and maximal running speed. In addition, we still have no way of determining whether the animal is capable of the fine adjustments in the timing and duration of stimulation employed *in vitro* to maximise power output. Thus, power output *in vivo* during burst running may be constrained by limits to the pattern of activation by the neuromuscular system. The importance of constraints such as this may differentially affect locomotor capacity at different stages of development. Thus, an explanation for the relationship between running velocity and body size involves a complex interaction between maximum available power (measured *in vitro*), limb morphology and the constraints imposed by gravitational forces (inertial loading) and limits to biological design.

References

ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1990). Scaling effects on muscle function: power output of isolated fish muscle fibres performing oscillatory work. *J. exp. Biol.* **151**, 453–467.

ARCHER, S. D., ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1990). Scaling effects on the neuromuscular system, twitch kinetics and morphometrics of the cod, *Gadus morhua*. *Mar. Behav. Physiol.* **17**, 137–146.

BENNETT, A. F., GARLAND, T. AND ELSE, P. L. (1989). Individual correlation of morphology, muscle mechanics and locomotion in a salamander. *Am. J. Physiol.* **256**, R1200–R1208.

CANNELL, M. B.(1986). Effect of tetanus duration on free calcium during the relaxation of frog skeletal muscle fibres. *J. Physiol.*, *Lond.* **376**, 203–218.

CURTIN, N. A. AND WOLEDGE, R. C. (1988). Power output and force–velocity relationship of live fibres from white myotomal muscle of the dogfish *Scyliorhinus canicula*. *J. exp. Biol.* **140**, 187–197.

GARLAND, T. (1982). Scaling maximal running speed and maximal aerobic speed to body mass in mammals and lizards. *Physiologist* **25**, 338.

GARLAND, T. (1983). The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool.*, *Lond.* **199**, 157–170.

GARLAND, T. (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurusnuchalis*. *J. Zool.*, *Lond. A* **206**, 425–439.

GLEESON, T. T., PUTNAM, R. W. AND BENNETT, A. F. (1980). Histochemical, enzymatic and contractile properties of skeletal muscle fibres in the lizard *Dipsosaurusdorsalis*. *J. exp. Zool.* **214**, 293–302.

GUNTHER, B. (1975). Dimensional analysis and theory of biological similarity. *Physiol. Rev.* **55**, 659–699.

HEGLUND, N. C., TAYLOR, C. R. AND MCMAHON, T. A. (1974). Scaling stride frequencies and gait to animals size: mice to horses. *Science* **186**, 1112–1113.

HERTZ, P. E., HUEY, R. B. AND NEVO, E. (1983). Homage to Santa Anita: Thermal sensitivity of sprint speed in agamid lizards. *Evolution* **37**, 1075–1084.

HILL, A. V.(1950). The dimensions of animals and their muscular dynamics. *Sci. Prog.* **38**, 209–230.

HUEY, R. B. (1982). Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. *Koedoe* **25**, 43–48.

Huey, R. B. and Hertz, P. E. (1982). Effects of body size and slope on sprint speed of a lizard (*Stellio* (*Agama*) *stellio*). *J. exp. Biol.* **97**, 401–409.

Jayne, B. C., Bennett, A. F. and Lauder, G. V. (1990). Muscle recruitment during terrestrial locomotion: how speed and temperature affect fibre type use in a lizard. *J. exp. Biol.* **152**, 101–128.

Johnson, T. P. and Johnston, I. A. (1991). Power output of fish muscle fibres performing oscillatory work: effects of acute and seasonal temperature change. *J. exp. Biol.* **157**, 409–424.

Josephson, R. K. (1975). Extensive and intensive factors determining the performance of striated muscle. *J. exp. Zool.* **194**, 135–154.

Josephson, R. K. (1985). Mechanical power output from striated muscle during cyclic contraction. *J. exp. Biol.* **114**, 493–512.

Josephson, R. K. and Stokes D. R. (1989). Strain, muscle length and work output in a crab muscle. *J. exp. Biol.* **145**, 45–61.

Josephson, R. K. and Young, D. (1987). Fiber ultrastructure and contraction kinetics in insect fast muscles. *Am. Zool.* **27**, 991–1000.

Losos, J. B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**, 1189–1203.

Losos, J. B., Papenfuss, T. J. and Macey, J. R. (1989). Correlates of sprinting, jumping and parachuting performance in the butterfly lizard, *Leiolepis belliani. J. Zool., Lond.* **217**, 559–568.

Losos, J. B. and Sinervo, B. (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. exp. Biol.* **145**, 23–30.

Marsh, R. L.(1988). Ontogenesis of contractile properties of skeletal muscle and sprint performance in the lizard *Dipsosaurusdorsalis. J. exp. Biol.* **137**, 119–139.

Marsh, R. L.(1990). Deactivation rate and shortening velocity as determinants of contractile frequency. *Am. J. Physiol.* **259**, R191–R196.

Marsh, R. L. and Bennett, A. F. (1985). Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the lizard *Dipsosaurus dorsalis. J. comp. Physiol.* B **155**, 541–551.

McMahon, T. A.(1974). Size and shape in biology. *Science* **179**, 1201–1204.

McMahon, T. A. (1975). Using body size to understand the structural design of animals: quadrupedal locomotion. *J. appl. Physiol.* **39**, 619–627.

McMahon, T. A.(1984). *Muscles, Reflexes and Locomotion.* Princeton: Princeton University Press.

Pennycuick, C. J. (1975). On the running of the gnu (*Connochaetes taurinus*) and other animals. *J. exp. Biol.* **63**, 775–799.

Rall, J. A. and Woledge, R. C. (1990). Influence of temperature on mechanics and energetics of muscle contraction. *Am. J. Physiol.* **259**, R210–R222.

Rayner, J. M. V. (1985). Linear relations in biomechanics: the statistics of scaling function. *J. Zool., Lond.* A **206**, 415–439.

Ready, N. E.(1986). Development of fast singing muscles in a katydid. *J. exp. Zool.* **238**, 43–54.

Rome, L. C., Funke, R. P., Alexander, R. M., Aldridge, H., Scott, F. and Freadman, M. (1988). Why animals have different fibre types. *Nature* **335**, 824–827.

Rome, L. C., Sosnicki, A. A. and Goble, D. A. (1990). Maximum velocity of shortening of three fibre types from horse soleus muscle: implications for scaling with body size. *J. Physiol., Lond.* **431**, 173–185.

Schmidt-Nielsen, K. (1984). *Scaling. Why is Animal Size Important?* London: Cambridge University Press.

Snell, H. L., Jennings, R. D., Snell, H. M. and Harcourt, S. (1988). Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evol. Ecol.* **2**, 353–369.

Snyder, R. C.(1954). The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *Am. J. Anat.* **95**, 1–47.

Sokal, R. R. and Rohlf, F. J.(1981). *Biometry.* San Francisco: Freeman.

Sukhanov, V. B. (1968). *General System of Symmetrical Locomotion of Terrestrial Vertebrates and Some Features of Movement in Lower Tetrapods.* Leningrad: Nauka Pub.

Swoap, S. J., Johnson, T. P., Josephson, R. K. and Bennett, A. F.(1993). Temperature, muscle power output and limitations on burst locomotor performance of the lizard *Dipsosaurus dorsalis. J. exp. Biol.* **174**, 185–197.

Wardle, C. S.(1975). Limit of fish swimming speed. *Nature* **255**, 725–727.