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ALLOMETRIC SCALING RELATIONSHIPS OF JUMPING PERFORMANCE IN THE STRIPED MARSH FROG *LIMNODYNASTES PERONII*

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Summary

We constructed a force platform to investigate the scaling relationships of the detailed dynamics of jumping performance in striped marsh frogs (*Limnodynastes peronii*). Data were used to test between two alternative models that describe the scaling of anuran jumping performance; Hill's model, which predicts mass-independence of jump distance, and Marsh's model, which predicts that jump distance increases as $M^{0.2}$, where M is body mass. From the force platform, scaling relationships were calculated for maximum jumping force (F_{max}), acceleration, take-off velocity (U_{max}), mass-specific jumping power (P_{max}), total jumping distance (D_J) and total contact time for 75 *L. peronii* weighing between 2.9 and 38.4 g. F_{max} was positively correlated with body mass and was described by the equation $F_{max}=0.16M^{0.61}$, while P_{max} decreased significantly with body mass and was described by the equation $P_{max}=347M^{-0.46}$. Both D_J and U_{max} were mass-independent over the post-metamorph size range, and thus more closely resembled Hill's model for the scaling of locomotion. We also examined the scaling relationships of jumping performance in metamorph *L. peronii* by recording the maximum jump distance of 39 animals weighing between 0.19 and 0.58 g. In contrast to the post-metamorphic *L. peronii*, D_J and U_{max} were highly dependent on body mass in metamorphs and were described by the equations $D_J=38M^{0.53}$ and $U_{max}=1.82M^{0.23}$, respectively. Neither model for the scaling of anuran jumping performance resembled data from metamorph *L. peronii*. Although the hindlimbs of post-metamorphic *L. peronii* scaled geometrically (body mass exponent approximately 0.33), the hindlimbs of metamorphs showed greater proportional increases with body mass (mass exponents of 0.41–0.42).

Key words: scaling, jumping performance, allometry, power, striped marsh frog, *Limnodynastes peronii*.

Introduction

Hill (1950) predicted that geometrically similar animals should run at the same speed and jump the same distance regardless of body size. However, because of the effects of not only body shape but also phylogenetic differences, the scaling relationships of locomotor performance for most terrestrial vertebrates are highly varied (Emerson, 1978; Huey and Hertz, 1982; Garland, 1983, 1984) and do not allow an adequate test of Hill's prediction. Because body shape is very conservative within the anurans and they appear to scale geometrically (Emerson, 1978; Marsh, 1994), they offer an ideal system for testing Hill's (1950) prediction. In contrast to Hill's (1950) model, Marsh (1994) suggested that, when our existing knowledge of anuran allometry and muscle contractile properties is considered, the jumping distance of anurans should not be expected to be mass-independent but rather scale to $M^{0.2}$, where M is body mass. Marsh (1994) attributes the differences between the two models to Hill's (1950) assumption that the intrinsic shortening velocity of hindlimb muscle scales as $M^{-0.33}$, while the empirically derived scaling relationship scales as $M^{-0.1}$.

From the available data on the scaling of anuran jumping performance, it appears that the scaling relationships more closely resemble the predictions outlined by Marsh (1994) and do not support Hill's (1950) prediction for the mass-independence of jump distance. Maximum jump distance scales interspecifically with an average mass exponent of 0.20 (Emerson, 1978; Zug, 1978; for a review, see Marsh, 1994). Intraspecific analyses report that jump distance scales with a mass exponent of between 0.18 and 0.36 (Rand and Rand, 1966; Emerson, 1978; Miller et al., 1993), with an even greater mass exponent for metamorphs (between 0.41 and 0.69) (John-Alder and Morin, 1990). However, several factors require that we do not reject Hill's (1950) model on the strength of these analyses alone. First, many of these intraspecific analyses used both metamorph and post-metamorph animals to derive scaling relationships even though metamorph animals appear to scale

differently from post-metamorph animals and bias scaling relationships towards higher mass exponents (Emerson, 1978; John-Alder and Morin, 1990). Moreover, only jump distance has been recorded and used to test between the two models of anuran jumping performance. Several other variables describing jumping performance should also vary predictably with body mass, such as maximum jumping acceleration and take-off velocity, and could be recorded and used to test between the two alternative models of scaling in anurans. Finally, several of the scaling analyses were only based on small sample sizes over a limited range of body sizes. Clearly, an intraspecific scaling analysis of jumping performance using a wide range of body sizes, and with the separate analyses of metamorph and post-metamorph animals, should be used to test between the two models of anuran jumping performance.

In this study, we used a force platform to investigate the allometric scaling relationships of jumping performance in post-metamorphic striped marsh frogs (*Limnodynastes peronii*) over a tenfold increase in body mass. A custom-designed force platform allowed the determination of the ground reaction forces of a jumping frog in all three dimensions of movement and the scaling relationships of maximal jumping force, acceleration, take-off velocity, jump distance, contact time on the ground and maximal instantaneous power output to be determined. Scaling relationships of metamorph *L. peronii* jumping were also investigated and compared with those of the post-metamorphic animals by recording their total jump distance over a sixfold increase in body mass. Both metamorph and post-metamorph relationships were used to test between Hill's (1950) and Marsh's (1994) models for the scaling of anuran jumping performance.

Materials and methods

Striped marsh frogs (*Limnodynastes peronii*) (Duméril and Bibron) of various sizes were collected from Melbourne and Boolarra, Victoria, Australia, during September 1996. The jumping performance of all frogs was assessed within at least 2 days of collection, after which they were released at their point of capture. Twelve *L. peronii* adults were collected in Brisbane and transported to the University of St Andrews, Scotland, UK, where a high-speed cine camera was used to validate the force platform experimentally. To examine the jumping performance of metamorph *L. peronii*, three foam nests were collected from Boolarra, Victoria, during January 1998 and placed in a 25 °C constant temperature room at The University of Queensland. The larvae were fed *ad libitum* on boiled lettuce until metamorphosis occurred. Jumping performance of the metamorphs was then assessed on the day after their tail had been completely resorbed.

The force platform

A custom-built force platform was constructed simultaneously to measure the vertical, horizontal and lateral ground reaction forces of a jumping frog (Fig. 1). The design of the force platform was based on that outlined by Katz and Gosline (1993) for measuring jumping performance in locusts. The platform consisted of a circular piece of balsawood (diameter 10.5 cm, width 8 mm) mounted on an L-shaped 10 mm×10 mm double-cantilever brass beam fixed to a solid wooden base. A sheet of sandpaper was attached to the surface of the platform to prevent the frogs from slipping during take-off. Three spring blades were cut from the brass supporting beams by machining 10 mm×8.8 mm holes at different orientations at 90° to each other, leaving only a wall thickness of 0.6 mm along each side of the 10 mm long spring blades. To detect changes in force in the three dimensions, 5 mm aluminium foil strain gauges were attached to the outer side of each spring blade. Each strain gauge, which corresponded to a separate dimension, formed a quarter of a bridge circuit that fed a signal directly into a Maclab bridge amplifier. Data were collected by a Maclab data-acquisition system which recorded at a sampling frequency of 1000 Hz. Data were recorded in the
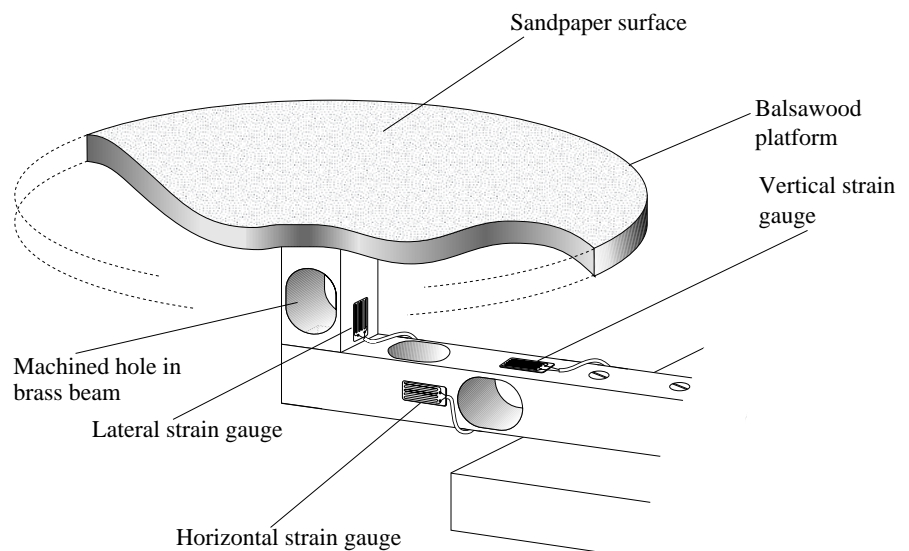

Fig. 1. Illustration of the force platform used to measure the ground reaction forces of striped marsh frogs (*Limnodynastes peronii*) during jumping. The diagram shows the three strain gauges (representing each dimension) that measured the force applied to the surface of the platform by a jumping frog.

Maclab version 3.5 software package using the accompanying Chart version 3.5.1 system with a 20 Hz low-frequency pass.

Mechanical crosstalk between the different dimensions was less than 5 % within the force range associated with this experiment and was not corrected for. Serial calibrations of the platform were conducted by placing known masses onto the platform at different orientations and applying known forces in each plane with the relationship between gravitational force and voltage output determined (vertical dimension 68.0 mV N^{-1}, both horizontal/lateral dimensions 44.8 mV N^{-1}).

Experimental validation of the force platform using high-speed cinematography

To validate experimentally the data obtained from the force platform, four *L. peronii* jumps were simultaneously assessed with high-speed cinematography and the force platform. High-speed cinematography has been used extensively in studies of fish and frog locomotion (Marsh and John-Alder, 1994; Temple and Johnston, 1998) and is considered an accurate method of measuring locomotor performance. Several jumping sequences were filmed with a 16 mm NAC E-10 high-speed cine camera at 500 frames s^{-1}, with four usable sequences analysed. Framing speeds for each sequence were verified by using timing marks that recorded at 100 Hz on the edge of the film. Three 400 W light sources supplied adequate illumination for filming. The camera was positioned to film a side-on view of a frog on the force platform from a distance of 2.5 m, which allowed movement in the vertical and horizontal directions to be filmed. Lateral movements were filmed by suspending a mirror at an angle of 45 ° behind the platform. Frogs were encouraged to jump off the platform by gently touching the urostyle with a pair of forceps whilst simultaneously filming and recording force platform output. The body temperature of the frogs was kept at 24 °C during experiments by holding them in a temperature-controlled water bath for at least 1 h before jumping and maintaining the room temperature between 20 and 25 °C. Film was developed 'open trap' and then viewed and analysed using a motion-analysis system (MOVIAS, NAC, Japan). The position of the approximate centre of mass (near the centre of the coccyx; Marsh and John-Alder, 1994) in all three dimensions was digitised to determine the distance moved whilst on the platform.

Four useable cine film sequences of frog jumps were analysed to determine take-off velocity, maximum acceleration and contact time. These cine film data were directly compared with values calculated from the force platform. Distance data were fitted with a sixth-order polynomial function to provide a smoothed curve from which velocity and acceleration could be calculated by differentiation. For each filmed frog jump, take-off velocity was estimated by taking the average of three velocity values centred on the frame at which take-off occurred. Maximum acceleration was estimated by using a moving average of three datum points over a period of 4 ms. Contact time was defined as the time at which movement was first detected until the point at which both feet left the platform.

Analysis of force-platform data

The three recorded signals were analysed separately to determine the ground reaction forces produced during each jump for each dimension. The lateral (F_L) and horizontal (F_H) forces were then summed *via* vector analysis to represent a single force trace in the horizontal dimension (F_{hl}). To determine the total force (F_{sum}) applied to the ground during jumping, the vertical (F_v) and horizontal forces (F_{hl}) were then summed *via* vector analysis. The maximum force produced was estimated by using a moving average of three consecutive datum points over a period of 2 ms.

To determine instantaneous lateral (A_L) and horizontal (A_H) acceleration, force values in the lateral (F_L) and horizontal dimensions (F_H) were divided by body mass (M) according to:

$$A_H = F_H/M, \qquad (1)$$

$$A_L = F_L/M. \qquad (2)$$

Acceleration in the vertical dimension (A_V) was calculated as:

$$A_V = (F_V - Mg)/M, \qquad (3)$$

where g is the acceleration due to gravity (in m s^{-2}).

Acceleration data were then used to calculate velocity by numerical integration, while the distance travelled by the centre of mass was calculated by numerical integration of the velocity data. Instantaneous power development (P) during a jump was calculated from the equation derived by Hirano and Rome (1984):

$$P = MgV_v + 0.5M[V^2t - V^2(t - 0.001)]/0.001, \qquad (4)$$

where V_v is instantaneous velocity in the vertical dimension, and V is the instantaneous vector sum of velocity.

Contact time (T_C) during a jump was taken as the total time from when a jump began (i.e. after acceleration increased for three consecutive readings) until the time when the vector sum of acceleration in all dimensions returned to zero. The total jump distance (D_J) of the frogs was estimated as:

$$D_J = [(V_{hl} \times 2 \times V_v)/9.8] + D_{hl}, \qquad (5)$$

where D_{hl} is the horizontal distance moved by the frog before take-off and V_{hl} is the vertical distance moved by the frog before take-off.

To estimate the muscle-mass-specific jumping power of *L. peronii* during maximal jumps, the hindlimb muscle mass as a proportion of total body mass was determined for four animals collected from Brisbane, Australia. Frogs were killed by a blow to the head, pithing and transection of the spinal cord. The hindlimb muscles were dissected away from the limbs, and total body mass and hindlimb muscle mass were determined on an A200S Sartorius analytical balance (±0.01 g).

Scaling relationships of jumping performance

The maximum jumping performance of 75 post-metamorphic *L. peronii* was assessed at 24 °C using the custom-designed force platform that measured the ground reaction forces of a jumping frog in three dimensions. As these frogs

included adult and sub-adult animals, they were referred to as post-metamophic frogs, which we defined as frogs that had not metamorphosed within the last few weeks before capture. We defined metamorph frogs in this study as those that had completely absorbed their tail within the last week. Jumps were elicited by pinching the urostyle with a pair of fine forceps, taking care to avoid applying forces to the platform. Each individual was stimulated to jump at least five times, with the jump that produced the greatest ground reaction force for each individual used as a measure of maximum jumping performance. The body temperature of the frogs was maintained at 24 °C for at least 3 h prior to experimental procedures by holding them in a shallow temperature-controlled water bath. The air temperature was maintained between 20 and 25 °C at all times, and the body temperature of the frogs did not change significantly during the jumping procedure. The body temperature of the frogs was determined by inserting a calibrated thermometer probe (±0.1 °C) into the cloaca.

As the resolution of the force platform did not allow the collection of useful data for metamorph jumps, only maximum jump distance was recorded for these animals. Each metamorph was encouraged to jump along a wooden bench by lightly touching its urostyle. The ventral surface of the metamorph frogs was kept wet at all times, allowing their jump distance to be recorded by measuring the distance between damp marks left on the wooden bench by the frogs. At least five jumps from each individual were recorded, and the longest jump for each individual was used as a measure of maximum jumping distance.

At the end of the jumping protocol, morphological measurements were taken for individual post-metamorphs and metamorphs. Snout-to-vent length (L_{SV}), femur (vent-to-knee length) (L_F) and tibia length (knee-to-ankle length) (L_T) were measured with Mitutoyo calipers to the nearest 0.2 mm. Mass was measured with an A200S Sartorius analytical balance (±0.01 g).

Calculations from metamorph jumping distance

Maximum take-off velocity, mass-specific power output and contact time were calculated from jumping distance from the set

of equations outlined by Marsh (1994). Calculations were based on the assumption that the angle of take-off to the horizontal was 45 °, a value close to the optimum angle of take-off. The position of the centre of mass at take-off was also assumed to have moved 1.2 times the length of the outstretched hindlimbs (Marsh, 1994). Average acceleration was calculated using the standard trajectory formulae outlined by Alexander (1968).

Statistical analyses

Allometric scaling relationships were expressed in the form $y=aM^b$, where M is body mass, a is the proportionality coefficient and b is the mass exponent. The equations were calculated using log-transformed data and least-squares regression techniques. Data collected from the high-speed cine film and the force platform were compared using Student's t-tests. All results are presented as means ± S.E.M. Significance was taken at the level $P<0.05$.

Results
Experimental verification of the force platform

Data were obtained simultaneously from the force platform and high-speed cine camera from four frog jumps. The two techniques produced statistically indistinguishable estimates of maximum velocity, maximum acceleration and total contact time (Table 1). Of the variables assessed, the greatest variation between the two techniques was in total estimated contact time, possibly because of the lower recording frequency and difficulty in determining the exact timing of initial movement in the cine film. It appeared that the force platform was at least as accurate at determining the jumping performance and the derived variables as data from high-speed cinematography. The advantages of the force platform are that it records the force build-up that must always precede movement and samples at a higher rate than the cine camera.

Jumping performance of post-metamorph frogs

The maximum jumping performance of 75 *L. peronii* weighing between 2.9 and 38.4 g was determined at 24 °C. A typical jump involved a rapid development of force resulting

Table 1. *Comparison of calculated values of take-off velocity, maximum acceleration and contact time for four* Limnodynastes peronii *jumps between data simultaneously collected from a force platform and high-speed cine camera (film)*

| | | Frog number | | | | |
		1	2	3	4	Mean ± S.E.M.
U_{max} (m s^{-1})	Film	3.41	2.24	2	1.28	2.24±0.44
	Platform	3.37	1.98	1.87	1.38	2.11±0.43
A_{max} (m s^{-2})	Film	95.9	43.7	40.8	32.6	53.3±14.4
	Platform	98	42.9	42.6	36.2	54.9±14.4
T_C (ms)	Film	58	84	64	54	65±6.6
	Platform	66	79	63	62	67.5±3.9

U_{max}, take-off velocity; A_{max}, maximum acceleration; T_C, contact time.
There were no significant differences between data collected from the force platform and high-speed cine camera ($P>0.05$).
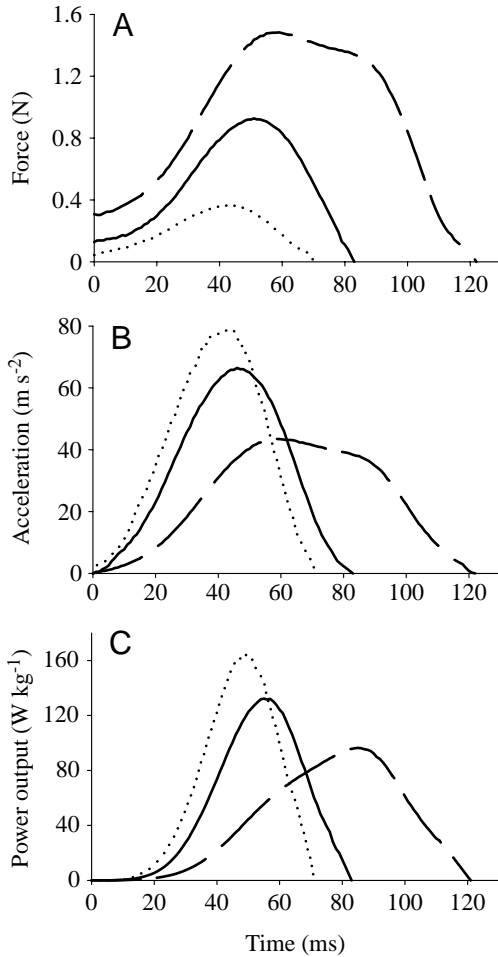
Fig. 2. Changes in (A) force, (B) acceleration and (C) instantaneous body-mass-specific power output during a typical maximal jump for three frogs of differing body mass at 24 °C measured with the force platform recording at 1000 Hz. Dotted, solid and dashed lines represent frogs of body mass 4.3, 12.8 and 30.8 g, respectively.

Fig. 3. Relationship between body mass (*M*) and (A) maximum jumping force (F_{max}) and (B) maximum jumping acceleration (A_{max}) for post-metamorphic striped marsh frogs (*Limnodynastes peronii*) weighing between 2.9 and 38.4 g recorded with a force platform at 1000 Hz.

in a peak ground reaction force after half to two-thirds of the total contact time and then a sharp decay of force to take-off (Fig. 2A). The entire jumping event was completed in a short time: the time from initial acceleration until take-off was
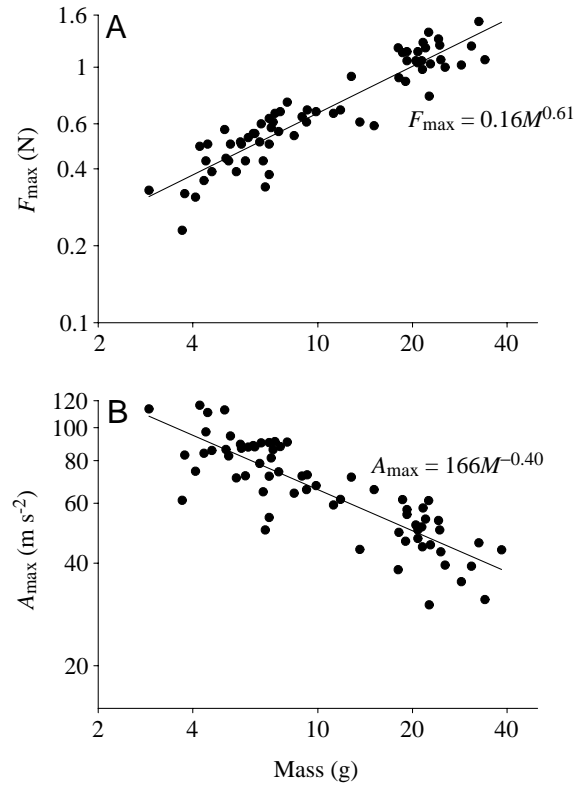
between 60 and 130 ms. Positive acceleration occurred throughout the entire phase of contact with the platform (Fig. 2B) and resulted in a maximum velocity at the instant of take-off. Instantaneous jumping power usually took longer to develop than force, with maximum power attained after approximately three-quarters of the total contact time (Fig. 2C).

Allometric scaling relationships were calculated for maximum jumping force (F_{max}), acceleration (A_{max}), take-off velocity (U_{max}), mass-specific jumping power (P_{max}), total

Table 2. *Relationships between body mass and various parameters of jumping performance in post-metamorphic striped marsh frogs (*Limnodynastes peronii*)*

		log*a*	*b*	r^2	*P*
Maximum force (F_{max})	N	−0.79±0.03	0.61±0.03	0.86	<0.001
Maximum acceleration (A_{max})	m s^{-2}	2.22±0.03	−0.40±0.03	0.73	<0.001
Contact time (T_C)	ms	−1.28±0.03	0.22±0.02	0.56	<0.001
Take-off velocity (U_{max})	m s^{-1}	0.45±0.04	−0.07±0.04	0.05	NS
Jump distance (D_J)	cm	−0.14±0.07	0.06±0.07	0.01	NS
Maximum instantaneous power (P_{max})	W kg^{-1} body mass	2.54±0.07	−0.46±0.06	0.44	<0.001

Equations are in the form $y=aM^b$, where *a* is the intercept at unity, *M* is body mass and *b* is the slope of the regression line.
Significance was taken at the level of *P*<0.05; NS, not significant.
Values are means ± s.e.m. (*N*=75).

jumping distance (D_J) and total contact time (T_C) on the platform (Table 2). F_{max} was positively correlated with body mass ($r^2=0.86$; $P<0.001$) and increased with a mass exponent of 0.61 (Fig. 3A). F_{max} increased from less than 0.4 N in the smaller frogs to more than 1.4 N in animals larger than 35 g. A_{max} was negatively correlated with body mass ($r^2=0.73$; $P<0.001$) and decreased with a mass exponent of −0.40 (Fig. 3B). Although the largest frogs only attained an A_{max} of less than 40 m s^{-2}, some of the smaller *L. peronii* reached accelerations greater than 100 m s^{-2}.

The mean U_{max} for *L. peronii* was 2.44±0.06 m s^{-1} and mean D_J was 0.87±0.03 m. U_{max} did not change significantly with body mass ($r^2=0.05$; $P>0.1$) and ranged from 1.6 to 3.5 m s^{-1} (Fig. 4A; Table 2). Although D_J appeared to increase with a body mass exponent of 0.06, there was no significant relationship between the two variables for animals weighing between 2.9 and 38.4 g ($r^2=0.01$; $P>0.1$; Fig. 4B; Table 2). P_{max} decreased significantly with body mass from close to 300 W kg^{-1} body mass in the small frogs to less than 100 W kg^{-1} in the larger animals (Fig. 4C; Table 2) ($r^2=0.44$; $P<0.001$). The contact time on the force platform was also highly dependent on the body mass of the animal and increased from less than 70 ms for the smaller animals to more than 120 ms for the larger animals ($r^2=0.56$; $P<0.001$) (Table 2).

The total proportion of body mass that was hindlimb muscle for adult *L. peronii* with an average body mass of 12.1±0.9 g was 19.1±1.2 %. Therefore, for a striped marsh frog of approximately 12 g, the total muscle-mass-specific power output during a maximal jump was approximately 620 W kg^{-1} of hindlimb muscle.

Jumping performance of metamorphs

Average jumping acceleration (A_{av}), U_{max}, P_{max} and T_C were calculated from recordings of maximum jumping distance for each metamorph. Over a threefold increase in body mass from 0.19 to 0.58 g, A_{av} was significantly related to the body mass of the metamorphs and scaled with a mass exponent of 0.38 (Table 3) ($r^2=0.14$; $P<0.05$). U_{max} was also highly dependent on body mass ($r^2=0.44$; $P<0.001$), ranging from 1.1 m s^{-1} to more than 1.6 m s^{-1} (Fig. 5A; Table 3). In addition, there was a significant relationship between D_J and body mass for *L. peronii* metamorphs ($r^2=0.67$; $P<0.001$) (Fig. 5B; Table 3). D_J
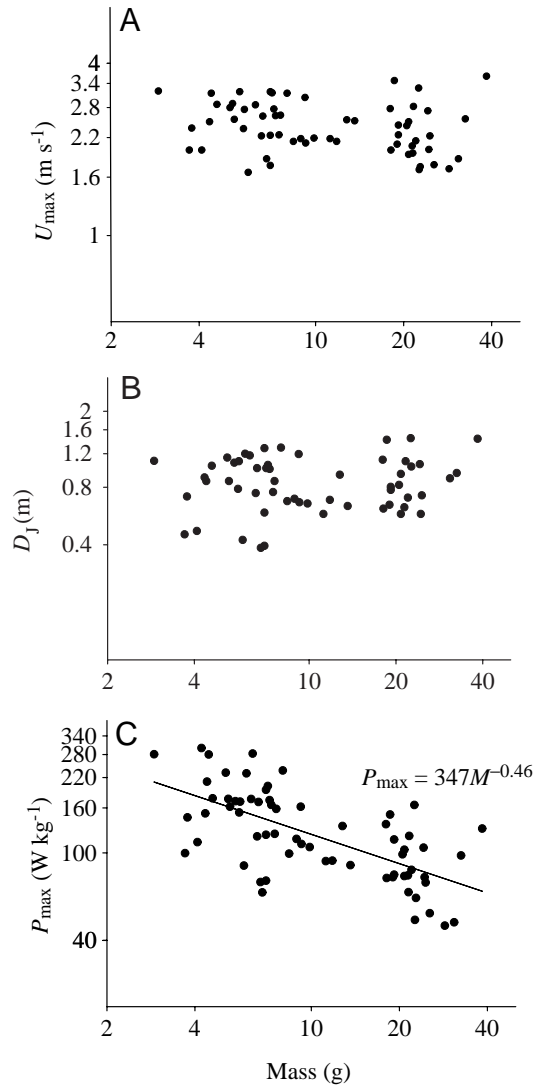
Fig. 4. Relationship between body mass (M) and (A) maximum take-off velocity (U_{max}), (B) maximum jump distance (D_J) and (C) maximum body-mass-specific jumping power (P_{max}) for post-metamorphic striped marsh frogs (*Limnodynastes peronii*) weighing between 2.9 and 38.4 g recorded with a force platform recording at 1000 Hz.

$$P_{max} = 347M^{-0.46}$$

Table 3. *Relationships between body mass and jumping performance parameters in metamorphs of the striped marsh frog* (Limnodynastes peronii)

		log$a$	b	r^2	P
Take-off velocity (U_{max})	m s^{-1}	0.26±0.02	0.23±0.04	0.44	<0.001
Jump distance (D_J)	cm	1.58±0.03	0.53±0.06	0.67	<0.001
Maximum power (P_{max})	W kg^{-1} body mass	1.99±0.06	0.31±0.11	0.18	<0.01
Average acceleration (A_{av})	m s^{-2}	1.90±0.08	0.38±0.16	0.14	<0.05
Contact time (T_C)	ms	−1.31±0.02	0.17±0.04	0.35	<0.001

Equations are in the form $y=aM^b$, where a is the intercept at unity, M is body mass and b is the slope of the regression line.
Significance was taken at the level of $P<0.05$.
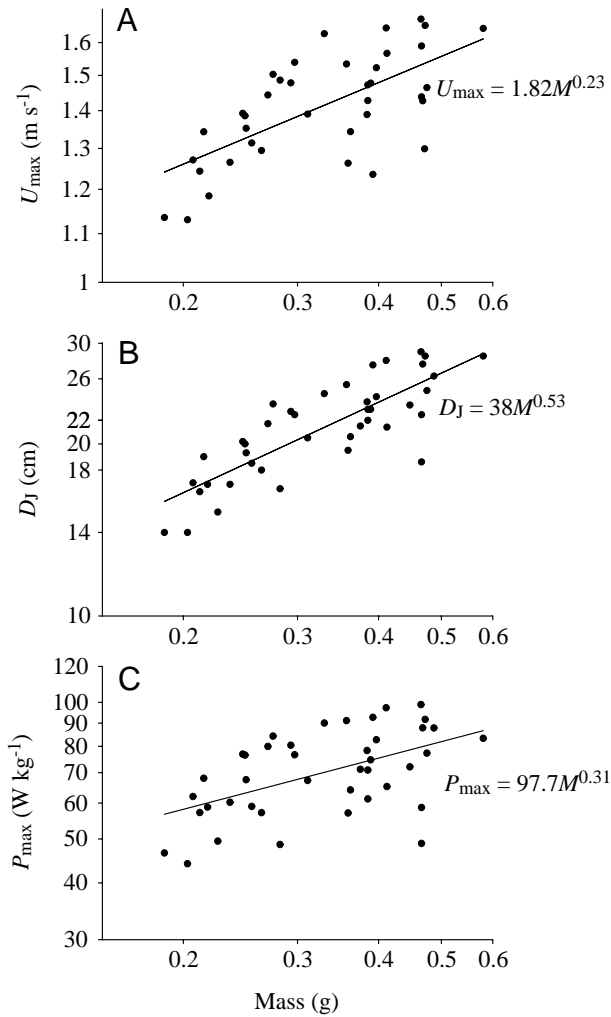Values are means ± S.E.M. ($N=39$).

Fig. 5. Relationship between body mass (M) and (A) maximum take-off velocity (U_{max}), (B) maximum jump distance (D_J) and (C) body-mass-specific jumping power (P_{max}) for metamorph striped marsh frogs (*Limnodynastes peronii*) weighing between 0.19 and 0.58 g calculated from jump distance.

increased from approximately 0.14 m for the smaller metamorphs to approximately 0.3 m for the larger animals. The P_{max} of metamorphs was also positively correlated with body mass and scaled with an exponent of 0.31 ($r^2=0.18$; $P<0.01$) (Fig. 5C; Table 3). P_{max} increased from around 45 W kg^{-1} body mass to more than 90 W kg^{-1} for the larger metamorphs.

The calculated T_C for the metamorphs was significantly correlated with body mass ($r^2=0.35$; $P<0.001$) and increased from approximately 35 ms for the smaller frogs to more than 45 ms for the larger metamorphs (Table 3).

Morphometrics

L_{SV}, L_F and L_T scaled geometrically with body mass, with a mass exponent of approximately 0.33 for post-metamorphic *L. peronii* (Table 4). The relationship between L_{SV} and body mass for metamorphs scaled with a body mass exponent of 0.28 ($r^2=0.83$; $P<0.001$), while L_F ($r^2=0.83$; $P<0.001$) and L_T ($r^2=0.83$; $P<0.001$) scaled with a much higher mass exponent of approximately 0.42.

Discussion
Scaling relationships of frog jumping

From the existing empirical data on isolated muscle performance and our knowledge of allometry in anurans, Marsh (1994) suggested that D_J in anurans should scale with a mass exponent of 0.20 and U_{max} and P_{max} should scale with exponents of 0.13 and 0.05, respectively. In contrast, Hill's (1950) model for scaling of anuran locomotion predicts U_{max} and D_J to be mass-independent (M^0), while P_{max} is expected to scale with an exponent of −0.33. From our data on the ground reaction forces of *L. peronii* during 'maximal' jumps, the scaling relationships of post-metamorph *L. peronii* appear to resemble more closely the predictions outlined by Hill (1950). There was no significant influence of body mass on either D_J or U_{max} of post-metamorph *L. peronii*, while P_{max} scaled with a mass exponent of −0.46. In contrast, the scaling relationships of jumping performance in metamorph *L. peronii* did not resemble either Hill's (1950) or Marsh's (1994) prediction for scaling of anuran jumping performance. Rather, D_J increased with a mass exponent of 0.53, while U_{max} and P_{max} scaled with exponents of 0.23 and 0.31, respectively. During this early stage of development, metamorph hindlimb length does not scale geometrically ($M^{0.33}$) like that of post-

Table 4. *Relationships between body mass, and snout–vent, femur and tibia length for metamorph and post-metamorphic striped marsh frogs (*Limnodynastes peronii*)*

y (mm)	Metamorphs					Post-metamorphs				
	N	$\log a$	b	r^2	P	N	$\log a$	b	r^2	P
L_{SV}	38	1.34±0.01	0.28±0.02	0.83	<0.001	75	1.37±0.01	0.32±0.01	0.98	<0.001
L_F	38	1.04±0.02	0.42±0.04	0.83	<0.001	51	1.00±0.01	0.29±0.01	0.92	<0.001
L_T	38	0.99±0.02	0.41±0.04	0.83	<0.001	51	0.85±0.02	0.34±0.01	0.92	<0.001

L_{SV}, snout–vent length; L_F, femur length; L_T, tibia length.

Equations are in the form $y=aM^b$, where a is the intercept at unity, M is body mass and b is the slope of the regression line.

Significance was taken at the level of $P<0.05$.

Values are means ± S.E.M. ($N=75$).

metamorph *L. peronii*, but scales with a greater exponent of approximately $M^{0.42}$.

From their extensive analyses of frog jumping, both Emerson (1978) and Zug (1978) reported interspecific allometry of D_J with a body mass exponent of between 0.03 and 0.49, with an average of approximately 0.2 (for a review, see Marsh, 1994). Intraspecific analyses suggest that D_J scales with a mass exponent of between 0.18 and 0.31 (Emerson, 1978). Miller et al. (1993) found the D_J of *Rana pipiens* to scale with a mass exponent of 0.36, while John-Alder and Morin (1990) found that the D_J of metamorph *Bufo woodhousii fowleri* increased with a body mass exponent of between 0.41 and 0.69. Thus, it appears that the scaling relationships of post-metamorph *L. peronii* jumping performance derived in this study are different from all previous analyses of anuran locomotion. However, when the data of Emerson (1978) are examined, the D_J for the adult size range of both *Bufo americanus* and *Pseudacris triseriata* appears to be independent of body mass. It is only when the juvenile data are included in the allometric relationship that D_J increases with body mass. Emerson (1978) states that the relationship between D_J and mass for these species is not linear when juveniles are included and may represent two independent scaling relationships. Similarly, when the D_J of metamorph *L. peronii* is combined with post-metamorph data, D_J for all *L. peronii* (over a mass range of 0.18–38.4 g) scales with a mass exponent of 0.37 (Fig. 6), which is a similar mass exponent to that reported in previous studies (Emerson, 1978; Marsh, 1994; Zug, 1978). It is possible that the scaling relationships of jumping performance in anurans that have been empirically derived may have been influenced by the inclusion of two different stages of development that are affected differently by body mass. Further research into the intraspecific scaling relationships of jumping performance in metamorph and post-
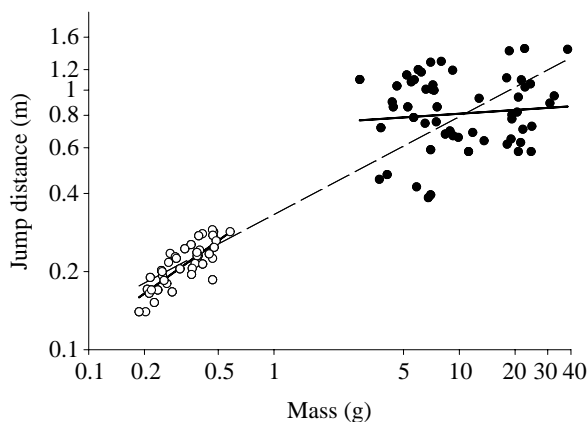
metamorph anurans is essential for determining whether the differences among our results for *L. peronii* and other analyses reflect general differences between the two developmental stages or are unique to *L. peronii*.

The scaling relationships of maximal locomotor performance vary widely between different groups of terrestrial animals, with no allometric model for locomotion describing all groups. Katz and Gosline (1993) analysed the ontogenetic scaling of the dynamics of jumping performance in the African desert locust (*Schistocerca gregaria*) using a force platform, a study that offers the most detailed comparison with the platform data on *L. peronii*. The U_{max} of the desert locust was independent of mass for the different developmental stages, while their F_{max} and A_{max} scaled with mass exponents of 0.73 and −0.27, respectively. Similarly, the U_{max} for post-metamorph *L. peronii* was mass-independent and F_{max} scaled as $M^{0.61}$ and A_{max} scaled as $M^{-0.40}$. P_{max} also scaled negatively for both *S. gregaria* ($M^{-0.17}$) and *L. peronii* ($M^{-0.46}$). Similar to both *L. peronii* and *S. gregaria*, Carrier (1995) found that the take-off velocity of black-tailed jackrabbits (*Lepus californicus*) during a standing jump was mass-independent over the size range 500–2000 g, and average acceleration was negatively correlated with body mass. Total T_C on the platform for *S. gregaria* varied between 12 and 65 ms and scaled with a mass exponent of 0.28. Similarly, the T_C for *L. peronii* post-metamorphs scaled at $M^{0.22}$, which probably reflected both the increase in hindlimb length and the decrease in A_{max} with body mass (Marsh, 1994). This scaling relationship for T_C is similar to that predicted for anurans from *in vivo* muscle performance (Marsh, 1994).

The ecological importance of jumping performance in many amphibians is likely to be related to predator avoidance and prey-capture success (see Marsh, 1994). Several authors have speculated as to which parameter of jumping performance most influences predator avoidance or prey-capture success (Emerson, 1978; Scott and Hepburn, 1976; Jayne and Bennett, 1990; Watkins, 1996). Emerson (1978) suggested that the locomotor parameters that are length- or mass-independent are possibly the critical determinants of performance. The jumping acceleration of *Pseudacris triseriata* and *Rana pipiens*, calculated from data on jumping distance, was reported to be independent of mass (Emerson, 1978). Therefore, Emerson (1978) suggested that acceleration, or quickness of movement, is the critical parameter of jumping in most species of frogs because the maintenance of constant acceleration requires morphological specialisation and is energetically expensive. In contrast, A_{max} of post-metamorph *L. peronii*, determined from force-platform recordings, was negatively associated with body mass. U_{max} and D_J are the locomotor parameters in post-metamorph *L. peronii* that are mass-independent and are possibly the critical determinants of performance in this species. In contrast, metamorph *L. peronii* do not exhibit mass-independence for any jumping parameter studied, possibly indicating that they have not reached a critical level of performance, governed by their susceptibility to predation, for any jumping parameter.

Fig. 6. Relationship between body mass (M) and jump distance (D_J) for both metamorph (open circles) and post-metamorphic (filled circles) striped marsh frogs (*Limnodynastes peronii*). Linear regressions are plotted for metamorph and post-metamorph data separately (solid lines; see Tables 2, 3), and for all data pooled (broken line). The equation for the regression through the pooled data is $D_J = 0.34M^{0.37}$ ($r^2 = 0.83$, $P < 0.001$).

Ontogenetic changes in the scaling relationships of jumping performance in *L. peronii* may be related to increased selection on juvenile performance and relaxed selection on adult animals. Although most juveniles of a species are slower and less agile than adults, they not only must still avoid the same predators as adult animals but also many other smaller gape-limited predators that the adults have outgrown. As a consequence, juveniles tend to be captured more regularly and experience higher mortality rates than adult animals (Williams, 1996; Arnold and Wassersug, 1978; Wassersug and Sperry, 1977), with selection on locomotor performance probably being stronger for these juvenile stages (Carrier, 1996). Consistent with these expected patterns of selection is the positive relationship between D_J and body mass in metamorph *L. peronii* and the size-independence of D_J in post-metamorphs. Several studies have reported considerable selection for larger body size in metamorph anurans (Wilbur and Collins, 1973; Wilbur, 1977; Werner, 1986). If this selection for increased body size is associated with selection for increased jump distance, then there should be a positive correlation between body size and jumping performance in the juvenile stage (as observed for metamorph *L. peronii*). In contrast to the metamorphs, post-metamorphic *L. peronii* may have grown too large for most size-limited predators and experience relaxed selection on both body size and jumping performance. Thus, a positive correlation between body size and jumping performance would not be expected for the post-metamorph *L. peronii*. Although this adaptive scenario is highly speculative, it forms a basis for future studies on ontogenetic variation in the selection of both body size and jumping performance, and its allometric consequences, in natural populations of *L. peronii*.

Jumping performance of Limnodynastes peronii

The highest body-mass-specific jumping power recorded for *L. peronii* post-metamorphs from the force platform was approximately 300 W kg^{-1} body mass, while average power output was 45–50 % of the maximum. The only comparable force-platform studies of jumping in frogs are for *Rana temporaria* (Calow and Alexander, 1973) and *Rana pipiens* (Hirano and Rome, 1984). Unfortunately, both these studies appear to have recorded only sub-maximal jumps, because other studies have documented jump distances that were almost double those reported in the force-platform work whilst using the same species (for a review, see Marsh, 1994). Calow and Alexander (1973) measured the ground reaction forces of a single foot during jumping in *Rana temporaria* and reported take-off velocities of up to 1.8 m s^{-1}, which are at the lower end of the ranges of velocities calculated for *L. peronii*. Similarly, Hirano and Rome (1984) report take-off velocities of approximately 1.4 m s^{-1} and maximum power outputs of 60 W kg^{-1} for *Rana pipiens*. Marsh (1994) reported power outputs of 170 W kg^{-1} for *Rana pipiens*, which is almost half those obtained here for smaller post-metamorph *L. peronii*. However, this difference may be attributable to the size of the

frogs used in each study. Marsh and John-Alder (1994) reported a peak jumping power output of approximately 70 W kg^{-1} in a 31 g Cuban tree frog (*Osteopilus septentrionalis*), a peak power output similar to that found in post-metamorphic *L. peronii* of similar body mass. Since power output during jumping is almost entirely derived from the hindlimbs, the muscle-mass-specific jumping power for the smallest *L. peronii* post-metamorphs is in excess of 900 W kg^{-1}. These estimates of muscle-mass-specific power output are conservative estimates because not all the hindlimb muscles are involved in jumping.

Maximum power output during jumping, as measured *in vivo*, is usually more than twice that available from direct muscle contraction alone (Marsh, 1994). The highest reported muscle power outputs from *in vitro* isotonic contractions of anuran muscles are approximately 360 W kg^{-1} muscle mass for *Xenopus laevis* (Lannergren et al., 1982). However, most recordings of *in vitro* muscle performance have found substantially lower maximum power outputs of between 150 and 250 W kg^{-1} (Marsh, 1994). Peplowski and Marsh (1997) suggested that the power output of hindlimb muscles in the Cuban tree frog (*Osteopilus septentrionalis*) was increased by elastic energy storage during jumping and that this could be the possible reason for the discrepancy between the calculated power required for take-off and values obtained from *in vitro* studies that determined the power available from the hindlimb muscles. Using electromyograhy and sonomicrometry, Olson and Marsh (1998) found that many of the hindlimb muscles, including the semimembranosus, gracilis major, cruralis and plantaris longus, are active 20–40 ms before the frog produces visible movement. They suggested that this supports the hypothesis that energy may be stored in some muscle groups in frog hindlimbs prior to take-off to help boost the power of the jump instantaneously (Olson and Marsh, 1998). If a large proportion of the power produced during jumping in *L. peronii* is actually derived from elastic stores, it is possible that the scaling relationships of jumping performance in post-metamorph *L. peronii* observed at the whole-animal level may also be a reflection of the scaling of the elastic storage properties of the muscle–tendon units. Thus, the use of our existing knowledge of allometry in anurans and the performance of isolated muscle may not accurately predict the scaling relationships of jumping performance in anurans.

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